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The Influence of River Discharge on Fishes and Invertebrates Associated with Small Oil and Gas Platforms in Nearshore Louisiana

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THE INFLUENCE OF RIVER DISCHARGE ON FISHES AND INVERTEBRATES ASSOCIATED WITH SMALL OIL AND GAS PLATFORMS IN NEARSHORE LOUISIANA

A Dissertation

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This dissertation is dedicated to my mom, the strongest and most selfless person I know.

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ABSTRACT

The nearshore region off Louisiana's coast is one of the most productive areas in the United States. Nutrient-rich discharge from the Mississippi and Atchafalaya rivers forms the base of this productivity, but it also contributes to the annual formation of a large hypoxic zone (DO < 2.0 mg l^{-1}). This region contains >900 oil and gas platforms (platforms) that are *de facto* artificial reefs and support fish and invertebrate communities. In this dissertation, I examined how select platform-associated fishes and invertebrates responded to river-driven productivity and hypoxia. Settlement plates were used to compare barnacle production at depths of 2 and 7-m along a 43.9 km landward-seaward transect with decreasing river influence. *Amphibalanus reticulatus* settlement and growth decreased with increased distance from shore and was generally higher at 2 than 7-m. Total accumulation of fouling organisms decreased at rates of -9.8 to -1.2 g m^{-2} d^{-1} km^{-1}, depending on depth and year. A video array was used to estimate abundances and depth distributions of fishes before, during, and after summer hypoxia at platforms experiencing intense (seaward) and mild hypoxia (shoal). Occupation of bottom waters by fishes was consistent throughout the study period at shoal platforms, but fishes were rarely observed in the bottom 3-m when hypoxia was present at seaward platforms. However, patterns of fish abundances were not driven by the presence or absence of hypoxia. A different camera array was used to characterize fish foraging at platforms. Sheepshead, Gray Snapper, Horse-eye Jack, Atlantic Spadefish, and Black Drum were observed foraging on fouling organisms, but Sheepshead was the only fish that consistently foraged on platforms (88.9% of samples). Mixing-models of Sheepshead stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) indicated their diet was not negatively affected by hypoxia, but gut contents suggested they temporarily exploited prey that were vulnerable because of hypoxia. Barnacles represented 64.1% of gut contents and stable

isotopes suggested that barnacles and filamentous algae were 79.2 – 83.0% of their prey. Secondary production at platforms was increased by high primary productivity associated with river discharge. However, hypoxia influenced distributions of platform-associated organisms and temporarily increased Sheepshead exploitation of benthic prey.

CHAPTER 1: INTRODUCTION

Nutrient discharge from the Mississippi and Atchafalaya rivers drives prolific primary production off Louisiana's coast (Lohrenz et al. 1990, 1997, 1999; Turner and Rabalais 1991; Dortch and Whitledge 1992; Rabalais et al. 1996), which results in high fisheries productivity (Gunter 1963). This region accounted for 10.8% of all U.S. commercial fisheries landings by weight from 2006–2015, and was only second to Alaska (NMFS 2017). However, nutrient discharge from the Mississippi and Atchafalaya rivers also leads to the seasonal formation of coastal hypoxia (DO < 2 mg l^{-1}; Turner and Rabalais 1991, 1994; Turner et al. 2006), which spans 15,100 – 18,000 km^2 (Obenour et al. 2013) and is considered the second largest hypoxic zone in the world (Rabalais et al. 2002). Hypoxia is known to decimate benthic communities (Dauer et al. 1992; Pihl 1994; Baustian and Rabalais 2009) and displaces mobile organisms (Leming and Stuntz 1984; Renaud 1986; Craig and Crowder 2001, 2005; Craig et al. 2005; Switzer et al. 2009, 2015; Craig and Bosman 2013), but the overall effect of hypoxia is unclear (Chesney et al. 2000; Chesney and Baltz 2001).

Historical river discharge on Louisiana's shelf and the associated high primary and secondary productivity is foundational for oil and gas exploration. This region exports about $152 billion in goods and services annually, most of which is related to oil and gas extraction (Barnes et al. 2015). Large reserves of oil and gas off Louisiana's coast resulted from burial of ancient riverine sediments deposited over 100 million years ago (Austin et al. 2004). Oil and gas exploration has substantially modified Louisiana's marine habitats since the mid-twentieth century. The most dramatic modifications were the installation of massive oil and gas infrastructure (platforms, pipelines). Currently, there are >2,000 oil and gas platforms on the Outer Continental Shelf of the northern Gulf of Mexico (BOEM 2017).

Oil and gas platforms (platforms) serve as small islands within the northern Gulf of Mexico (nGOM) where fishermen tie up, birds land, and marine biota (algae, invertebrates, fishes, etc.) aggregate. Platforms are *de facto* artificial reefs that attract large assemblages of fishes (Shinn 1974; Duglas et al. 1979; Harville 1983; Figure 1.1) and invertebrates (Gunter and Geyer 1955; Gallaway et al. 1981; Lewbel et al. 1987; Reeves et al. 2017; Figure 1.2). At one time, platforms account for ~12 km^2 of hard bottom substrate on the shelf (Gallaway et al. 1998), and are renowned fishing destinations where reef-associated fishes are commonly landed (Stanley and Wilson 1989). The number of platforms in federal waters peaked at ~4,000 in 2008 and has decreased to ~2,100 in 2017 (BOEM 2017).

Figure 1.1: Atlantic Bumper *Chloroscombrus chrysurus*, Gray Triggerfish *Balistes capriscus*, Blue Runner *Caranx crysos*, Red Snapper *Lujanus campechanus*, and Gray Snapper *Lutjanus griseus* around an oil and gas platform (SS 144-1) in July of 2015.

The value of platforms as artificial reef habitat has long been the subject of debate (Polovina 1991; Grossman et al. 1997; Cowan et al. 2011), but it is critical to resolve this debate

since nearshore platforms are rapidly being removed. Questions surrounding the ecological value of platforms fall within the broader attraction vs. production artificial reef debate. The attraction side argues that artificial reefs attract fishes and make them more susceptible to fishing (Stone et al. 1979), while the production side argues that artificial reefs produce additional fish biomass (Samples and Sproul 1985; Bohnsack 1989). The explanation is probably not monothetic and both processes are likely involved (Bohnsack 1989), and the degree of attraction and/or production is unquestionably taxon-specific. For example, platforms are likely to support secondary production of Sheepshead (*Archosargus probatocephalus*) that graze biofouling, but may not result in significant reef driven production of other fishes such as Red Snapper (*Lutjanus campechanus*; Cowan and Rose 2016). Since platforms are removed after their production life ends (Kaiser 2006) and removals are especially high in nearshore waters (total depths < 15 m; Pulsipher et al. 2001), it is important to resolve this debate and to determine if loss of these structures needs to be mitigated.

1.1. Review of Existing Research About the Ecology of Platforms in the Gulf of Mexico

I reviewed 50 peer reviewed papers about the ecological aspects of platforms in the nGOM (Table 1.1; Appendix A). Research started around the mid-twentieth century (Gunter and Geyer 1955) and topics ranged from foraminifera assemblages (Gupta and Smith 2013) to characterizing food webs (Gallaway et al. 1981; Daigle et al. 2013). Most studies were descriptive and focused on characterizing fish (36%) and invertebrate assemblages (18%), and 24% of all studies were focused on the ecology of Red Snapper. Relatively few studies were focused on productivity and food webs (6%). Of those, studies characterized secondary production of amphipods (Beaver et al. 2003) and food webs using gut contents of fishes (Gallaway et al. 1981) and $\delta^{13}C$ and $\delta^{15}N$ of a variety of fishes and invertebrates (Daigle et al.

2013). These studies have expanded our knowledge of the ecological function of platforms, but information gaps remain.

Figure 1.2: Tagged stone crab *Menippe adina* on an oil and gas platform that was covered with barnacles, tunicates, and sponges in the August of 2015.

Developing a better understanding of platform related food webs and productivity is key for resolving the debate surrounding the ecological value of platforms in the northern Gulf of Mexico. Barnacles are the dominant fouling organisms on nearshore platforms (Gunter and Geyer 1955; Lewbel et al. 1987; Reeves et al. 2017), and they provide structural habitat (microtopographic relief) for other organisms, such as stone crabs (*Menippe* spp.; Reeves et al. 2017). Barnacles are filter feeders that consume zooplankton and phytoplankton (Barnes 1959), and their growth and settlement is positively associated with productivity (Menge et al. 1997, 2003; Sanford and Menge 2001). Understanding food web pathways and production associated with artificial reefs is critical to resolving the attraction vs. production debate (Bohnsack 1989),

Table 1.1: Study themes, number of studies, and percentage of studies about the ecology of platforms in the Gulf of Mexico from the 50 reviewed papers. Only peer-reviewed papers were included in the review. Papers were selected using the following search terms in Web of Science and by scouring their works cited sections: "oil and gas platforms Gulf of Mexico," oil and gas platforms Gulf fish," "oil and gas platforms Gulf invertebrate." Since some papers had multiple objectives (i.e. characterize fish and invertebrate assemblages), the number of studies does not sum to 50.

Study Theme	**Number of Studies**	**Percentage of Studies**
Fish Ecology		
Fish Assemblages	18	36
Red Snapper Life History and Movement	9	18
Hydroacoustic Surveys	5	10
Red Snapper Feeding Ecology	3	6
Blue Runner Movement	1	2
Blue Runner Feeding Ecology	1	2
Fouling Organism Ecology		
Invertebrate Assemblages	9	18
Coral Genetics	2	4
Foraminifera Assemblages	1	2
Stone Crab Density and Life History	1	2
Invertebrate PAH Concentrations	1	2
Productivity and Food Webs		
Food Webs	2	4
Secondary Production	1	2
Review Papers	3	6

and it has received increased attention in recent years. Recent studies of offshore platforms in the GOM have examined the importance of fouling organisms as prey for fishes (Daigle et al. 2013; Foss 2016; Schwartzkopf et al. 2017), and have shown that they are critical prey and ecological engineers at platforms off California's coast (Page et al. 1999; Claisse et al. 2014). However, the magnitude of primary and secondary production at platforms in the nGOM and

their role in platform food-webs is still poorly understood, and this is key to determining the ecosystem services provided by platforms.

The vertical extent of platforms may also provide reef-associated organisms with a number of distinct benefits including increased potential for production and refuge from hypoxia. Platforms span from the seafloor to above the surface. This vertical structure allows barnacles and other fouling organisms to colonize the highly productive surface waters (Reeves et al. 2017) where sunlight, nutrients, and plankton are plentiful. Platforms may also benefit reef-associated organisms by providing hard bottom substrate in the oxygenated waters overlaying hypoxic bottom waters. Hypoxia is believed to alter abundances of some reef-associated fishes and result in their vertical redistribution (Stanley and Wilson 2004), but few studies have focused on how the distributions of reef-associated organisms respond to hypoxia (e.g. Lenihan et al. 2001; Stanley and Wilson 2004).

1.2. Objectives of this Dissertation

In this dissertation, I explore some unique ecological aspects of oil and gas platforms and how the ecology of platforms is affected by river discharge. Chapter 1 examines how barnacle production varies at platforms across a 43.9 km landward-seaward transect with declining freshwater influence. Chapter 2 examines how the distribution and abundances of fishes around platforms respond to hypoxia. Chapter 3 examines the foraging behavior of reef associated fishes and documents how fouling organisms are affected by hypoxia. Chapter 4 examines how the diets of Sheepshead *Archosargus probatocephalus* and stone crab *Menippe adina* change in response to hypoxia, and documents the degree to which platform-dwelling fauna are prey.

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CHAPTER 2: BARNACLE SETTLEMENT AND GROWTH AT OIL AND GAS PLATFORMS IN THE NORTHERN GULF OF MEXICO[1]

2.1. Introduction

Nutrient discharge from the Mississippi and Atchafalaya rivers drives prolific primary production off Louisiana's coast (Turner & Rabalais 1991; Dortch & Whitledge 1992; Rabalais et al. 1996). This region produces > 73% of all U.S. fisheries landings in the Gulf of Mexico (GOM; NMFS 2015), and leads in commercial landings of many reef-associated species [Red Snapper (*Lutjanus campechanus*), Lane Snapper (*Lutjanus synagris*), Vermillion Snapper (*Rhomboplites aurorubens*), Warsaw Grouper (*Epinephelus nigritus*); NMFS 2015]. Naturally-occurring hard bottom habitat is rare on the continental shelf off Louisiana (Parker et al. 1983), and shelf edge banks provide the only source of natural hard bottom substrate. However, oil and gas platforms (platforms) are *de facto* artificial reefs that accounted for ~12 km^2 of hard bottom substrate on the shelf (Gallaway et al. 1998), and are renowned fishing destinations where reef-associated fishes are commonly landed (Stanley & Wilson 1989). The number of platforms in the GOM peaked at ~4,000 in 2008 and has decreased to ~2,100 in 2017 (BOEM 2017).

The value of platforms as artificial reef habitat has long been the subject of debate (Polovina 1991; Grossman et al. 1997; Cowan et al. 2011), but it is critical to resolve this debate since nearshore platforms are rapidly being removed. Questions surrounding the ecological value of platforms fall within the broader attraction vs. production artificial reef debate. The attraction side argues that artificial reefs attract fishes and make them more susceptible to fishing

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(Stone et al. 1979), while the production side argues that artificial reefs produce additional fish biomass (Samples & Sproul 1985; Bohnsack 1989). The explanation is probably not monothetic and both processes are likely involved (Bohnsack 1989), and the degree of attraction or production is unquestionably taxon-specific. For example, platforms likely result in the production of Sheepshead (*Archosargus probatocephalus*), but may not result in significant production of Red Snapper (*Lutjanus campechanus*; Cowan and Rose 2016).

Most platform research in the GOM has focused on offshore platforms (≥ 25 m total depth), but nearshore platforms (5 – 25 m total depth) may be especially important because they occupy the highly productive region influenced by the Atchafalaya and Mississippi rivers. Nearshore platforms represent ~40% of platforms in the GOM (BOEM 2017). These nearshore platforms host diverse assemblages of fishes that are associated with varying degrees of freshwater influence (Reeves 2015; Munnelly 2016). Barnacles are the dominant fouling organisms on nearshore platforms (Gunter & Geyer 1955; Lewbel et al. 1987; Reeves et al. 2017a), and they provide structural habitat (microtopographic relief) for other organisms, such as stone crabs (*Menippe* spp.; Reeves et al. 2017a) and amphipods (Beaver et al. 2003). Barnacles are filter feeders that consume zooplankton and phytoplankton (Barnes 1959), and their growth and settlement is positively associated with productivity (Menge et al. 1997; 2003; Sanford and Menge 2001). Understanding secondary production on artificial reefs is critical to resolving the attraction vs. production debate (Bohnsack 1989), and it has received increased attention in recent years. Recent studies of offshore platforms in the GOM have examined the importance of fouling organisms as prey for fishes (Daigle et al. 2013; Schwartzkopf 2014; Foss 2016) and as amphipod habitat (Beaver et al. 2003). While the importance of filter feeders as prey and

ecological engineers is well established for platforms off California's coast (Page et al. 1999; Claisse et al. 2014), platform-dwelling barnacles in the GOM have received little attention.

In this paper, we present a two-year study where settlement plates were used to examine how growth and settlement of platform-dwelling barnacles varied with distance from shore and depth. We hypothesized that barnacle growth and settlement is greater closer to shore and at shallower depths due to the higher degree of freshwater influence and eutrophication in this part of the coastal zone (Reeves 2015; Munnelly 2016; Reeves et al. 2017b).

2.2. Methods

Settlement plate construction and deployment

Settlement plates were constructed from 6 inch PVC schedule 40 pipe. The pipe was split lengthwise to make two pieces with concave and convex outer surfaces that were cut into 10 cm long sections. Individual 10 cm sections were considered settlement plates, and were mounted to platforms so that convex surfaces faced outwards. The outer 254 cm^2 surface area was used for all analyses.

A total of seventy-two settlement plates were deployed at 12 platforms (6 settlement plates/platform) along a 43.9 km landward-seaward transect starting ~15 km south of the Isles Dernieres, Louisiana in 2015 and 2016 (Figure 2.1, Table 2.1). Platforms were small (1 – 4 pilings) and located in depths of 7.6 – 33.5 m. Divers affixed two sets of three settlement plates at depths of 2 and 7 m. However, 2m plates were lost at the three most seaward platforms in both years (18 settlement plates). Settlement plate deployments lasted 92-125 days. Plates were retrieved by divers who sealed the plates in plastic bags while underwater to prevent the loss of loose materials. Settlement plates were kept on ice until frozen at ~ –18ºC.

In conjunction with settlement plate deployment and retrieval, we collected hydrographic profiles of the upper 8 m with a YSI 6820 V2 Sonde. The Sonde was lowered from the vessel at a rate of 0.04 ± 0.004 m/s (95% CI) and recorded temperature (ºC), salinity (PSU), and dissolved oxygen (mg L^{-1}) in two-second intervals. The Sonde was calibrated before and after each sampling trip using the manufacturer's specifications (YSI Incorporated 2012).

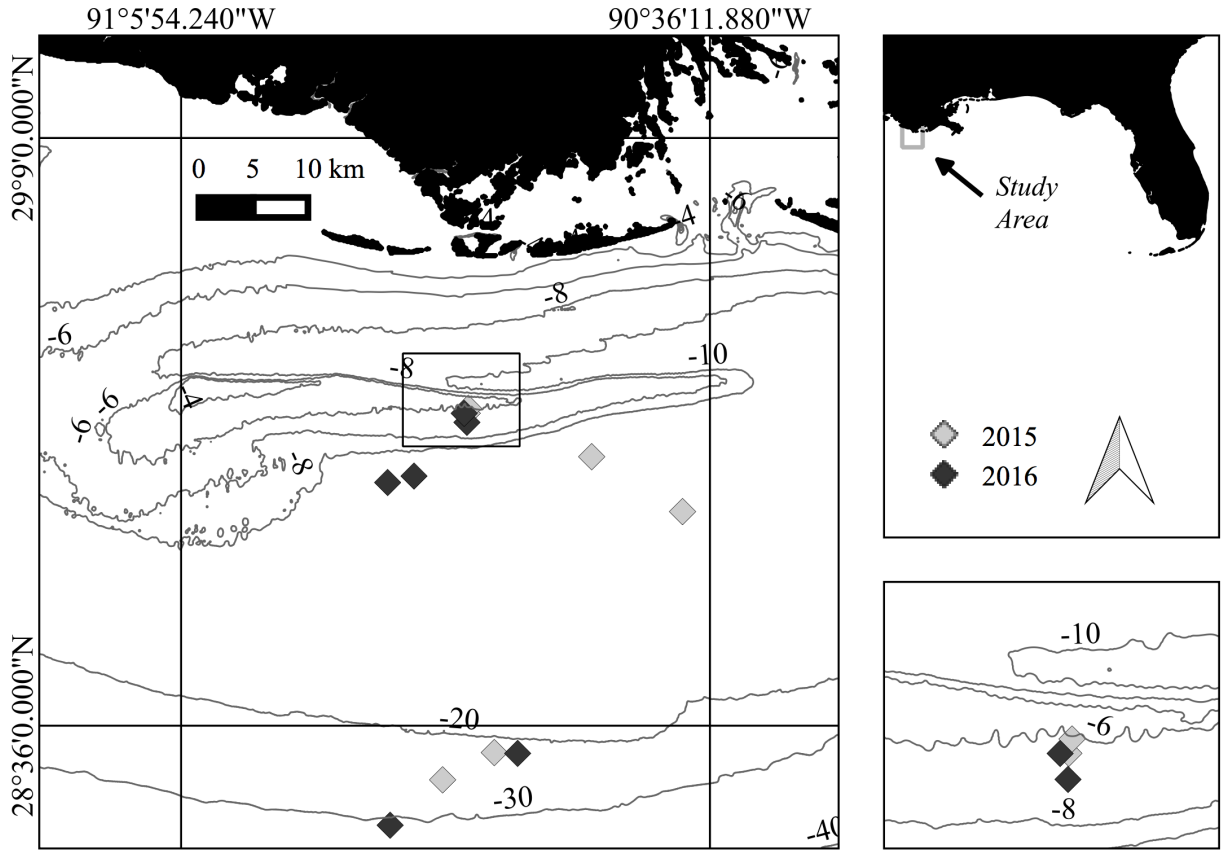

Figure 2.1. Locations of platforms where settlement plates were deployed in 2015 and 2016. The panel in the bottom right is an inset for the area demarked by the small rectangle in the main plot. Grey diamonds denote the locations of platforms sampled in 2015 and black diamonds denote the locations of platforms sampled in 2016. Numbers denote the total depth (m) of contour lines

Settlement plate processing

We subdivided each settlement plate into six equal cells and subsampled five barnacles (> 2 mm width) from each cell for biometrics (≥ 30 barnacles per plate). Barnacles were only

Table 2.1. Platform names, distances to shore, settlement plate deployment and recovery dates, and the total time of deployment (days).

Site Name	Distance from shore (km)	Total Depth (m)	Number of Pilings	Deployment Date	Recovery Date	Deployment Time (Days)
SS 93-44	15.7	7.6	2	Jul 29, 2015	Nov 4, 2015	98
SS 93-43	16.2	7.9	1	Jul 29, 2015	Nov 4, 2015	98
SS 93-61	16.2	7.9	1	Aug 19, 2016	Nov 21, 2016	94
SS 93-35	17.2	8.2	1	Aug 19, 2016	Nov 21, 2016	94
PL 21-1	21.4	17.3	1	Aug 28, 2015	Dec 1, 2015	95
SS 113-52	23.1	14.9	1	Aug 21, 2016	Nov 21, 2016	92
SS 112-4	23.7	14.6	2	Aug 19, 2016	Nov 21, 2016	94
ST 72-1	28.7	19.5	1	Aug 28, 2015	Dec 1, 2015	95
SS 189-C	51.6	22.6	1	Jul 29, 2015	Dec 1, 2016	125
SS 188-3	51.7	22.3	1	Aug 21, 2016	Nov 21, 2016	92
SS 209-P	54.6	29.9	4	Aug14, 2015	Dec 1, 2015	109
SS 215-C	59.6	33.5	1	Aug 21, 2016	Nov 21, 2016	92

subsampled if their bases were directly attached to the settlement plate. If empty cells were present, additional barnacles were sampled from adjacent cells so that sample size was as close as possible to 30 barnacles. Barnacles heights and widths were measured to 0.1 mm, total (shell + tissue) and tissue wet weights were measured to 0.001 g, and barnacles were identified to the species level. Settlement plates were then scraped of all fouling material, which was weighed to the nearest 0.1 g. Barnacles were then sorted by species and counted. *Amphibalanus reticulatus* and *Amphibalanus amphitrite* required dissections to distinguish species, and were thus grouped as *Amphibalanus* spp. for counts. Counted barnacles were categorized as spat ($\leq$ 2 mm width) or post-spat (>2 mm width). Barnacles used for biometrics were added to estimates of fouling material weight and barnacle counts.

After all settlement plates were sampled, we subsampled an additional five *A. reticulatus* from each plate to compare wet vs. dry tissue weights. *A. reticulatus* tissue wet weights were measured and barnacles were subsequently dried at 110ºC for 2 hours (Crisp & Patel 1961) and

weighed again. We did not include these barnacles in other comparisons of biometrics since this subsampling procedure differed from the original.

Statistical analyses

Barnacle abundances and biometrics were converted to rates by standardizing the following variables by time of deployment: fouling accumulation (g m^{-2} d^{-1}), post-spat and spat *Amphibalanus spp.* abundances (number m^{-2} d^{-1}), post-spat and spat *Megabalanus tintinnabulum* abundances (number m^{-2} d^{-1}), and *A. reticulatus* height (mm d^{-1}), width (mm day^{-1}), total wet weight (mg d^{-1}), and tissue wet weight (mg d^{-1}). Barnacle abundances were considered settlement rates, and *A. reticulatus* biometrics were considered proxies for growth rates. Since barnacles on an individual plate settled sometime after deployment of plates, growth rates are conservative estimates. It is also likely that barnacles on an individual plate settled at different times, so we interpreted growth rates for the entire plate, not individual barnacles.

Fouling accumulation (g m^{-2} d^{-1}), post-spat and spat *Amphibalanus spp.* abundances (number m^{-2} d^{-1}), post-spat and spat *M. tintinnabulum* abundances (number m^{-2} d^{-1}), and *A. reticulatus* height (mm d^{-1}), width (mm d^{-1}), tallness (height/width), total wet weight (mg d^{-1}), and tissue wet weight (mg d^{-1}) were compared across distance from shore (km), year (2016 vs. 2017), and depth (2 vs. 7 m) using generalized linear mixed models (GLMMs; Proc Glimmix; SAS 9.4) . We also used GLMMs to compare the ratio of tissue: total wet weight (percent tissue) across distance, year, and depth and included height as a covariate to account for size-specific differences. Every feasible combination of variables was considered for the comparisons listed above except for percent tissue. The model of percent tissue was selected using backward elimination because of the high number of possible variable combinations. Akaike's Information Criteria (AIC) was utilized to select final models. The model with the lowest AIC was selected

for comparisons of all feasible models, and backward elimination removed variables that did not reduce the percent tissue model's AIC. Backward elimination began with the full model and was used to remove interactions and main effects in order of complexity (most complex interactions were removed first). When there were models with competing AIC values (Δ AIC < 2; Bolker 2008), the model with fewer parameters was selected (Arnold 2002). Indicator variables were used for year (2015 = 1; 2016 = 0) and depth (2 m = 1; 7 m = 0). We also used simple linear regression to compare percent tissue vs. tallness and tissue wet weight vs. dry weight.

All statistical models were fitted with normal or lognormal distributions (identity link function) and assumptions were evaluated using predicted vs. residual plots. Random effects were used to designate individual platforms as the sampling unit for all analyses and a plate identifier was designated as a cluster for analyses of biometrics to control for the clustered nature of the data (Nelson 2014).

2.3. Results

Cross-shelf hydrography

Hydrographic data provided a snapshot of seasonal trends and indicated that hydrography varied with distance from shore on plate deployment and retrieval dates (Figure 2.2). With the exception of the 2015 deployment, salinity (PSU) generally increased with distance from shore and was higher on retrieval than deployment dates [Δ salinity at 5m (offshore – nearshore): -2.2 (2015 deployment); 3.5 (2015 retrieval); 1.6 (2016 deployment); 1.7 (2016 retrieval)]. There was strong salinity stratification (low salinity near the surface and high salinity at 7 m) at the platforms nearest to shore during the 2015 deployment. Salinity at 2m was substantially lower at nearshore vs. offshore, but salinity at 7m was higher at nearshore vs. offshore platforms. Salinity

stratification at these platforms corresponded with high DO (> 10 mg L^{-1}) near the surface and extremely low DO (< 0.5 mg L^{-1}) at 7 m. With the exception of the 2015 retrieval,

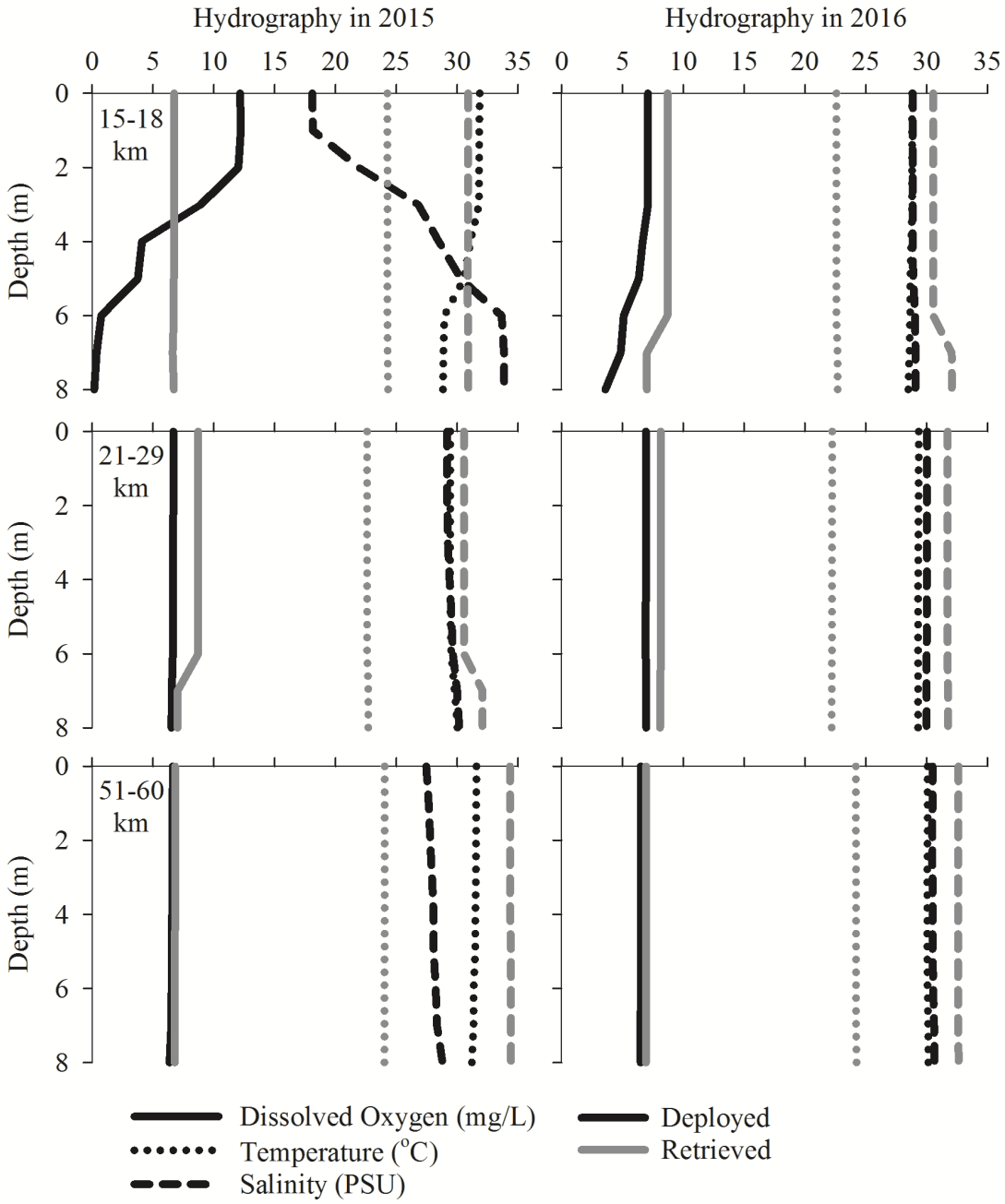

Figure 2.2. Depth profiles of DO (mg/L), temperature (ºC), and salinity (PSU) in 2015 and 2016 at platforms on days when settlement plates were deployed and retrieved. For this plot, platforms were grouped into three distance from shore categories (15 – 18, 21 – 29, 51 – 60 km). Black lines denote conditions on deployment dates and gray lines denote conditions on retrieval dates. All hydrographic variables are plotted against a single x-axis that represents variables and their respective units.

temperature (ºC) generally increased with distance from shore [Δ temperature at (offshore – nearshore): 0.9 (2015 deployment), -0.2 (2015 retrieval), 1.4 (2016 deployment), 2.1 (2016 retrieval)]. This trend was not observed during the 2015 retrieval because the settlement plates closest to shore were removed ~4 weeks earlier (Nov 4 vs. Dec 1) than those further offshore.

Cross-shelf fouling accumulation

Fouling accumulation decreased with increased deployment depth and distance from shore, and was higher in 2016 than 2015 (Figure 2.3; Table 2.2; Appendix B). Inclusion of the distance-by-depth by-year interaction indicated that separate regression lines were needed for each year- by-depth combination of plates (2015 & 2m, 2015 & 7m, 2016 & 2m, 2016 & 7m).

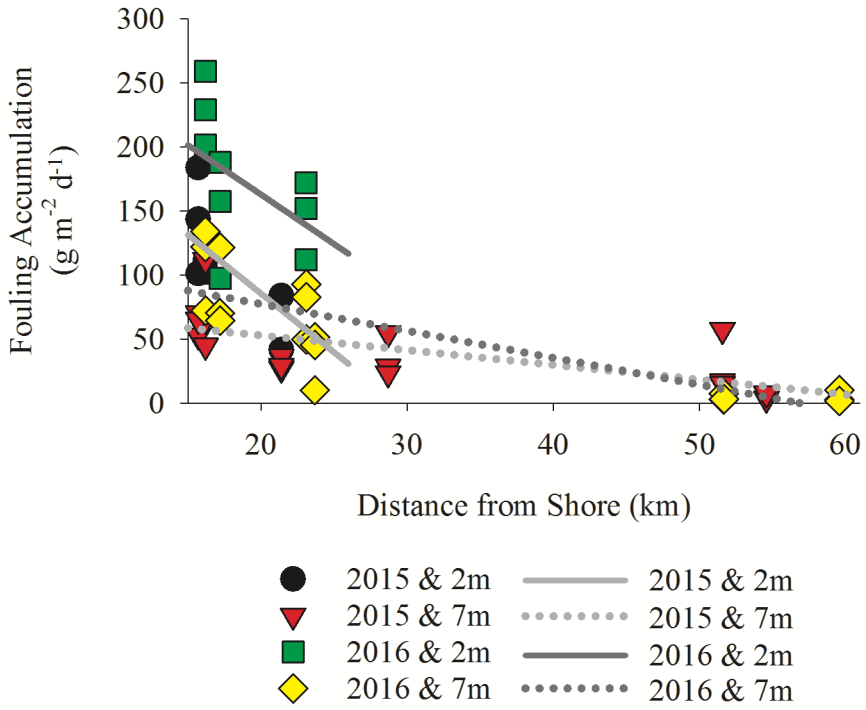

Figure 2.3. Patterns of fouling accumulation (g m^{-2} d^{-1}) for each year-by-depth combination of settlement plates (2015 & 2m, 2015 & 7m, 2016 & 2m, 2016 & 7m) with varying distance from shore. Regression lines were generated by the GLMM and were plotted for relationships identified as being important by AIC selection.

Table 2.2. Model intercepts (Int.), degrees of freedom error (D.F.), slopes (β) and their standard errors (SE) for variables included in generalized linear mixed models of fouling accumulation, barnacle counts, and barnacle biometrics. N.I.M is an abbreviation for "not in model." N.T. is an abbreviation for "not tested" and denotes that the variable was not evaluated for inclusion in that model. Indicator variables were used for year (2015=1; 2016=0) and depth (2 m= 1; 7 m=0). "Num." is an abbreviation for number and "wt." is an abbreviation for weight.

Response	**Int.**	**D.F.**	**Distance (km)** [β, (SE)]	**Depth (m)** [β, (SE)]	**Year (Yr)** [β, (SE)]	**km*m** [β, (SE)]	**km*Yr** [β, (SE)]	**m*Yr** [β, (SE)]	**km*m*Yr** [β, (SE)]	**Height** [β, (SE)]	**km*Height** [β, (SE)]
Fouling Accum. (g m^{-2} d^{-1})	119.510	4	-2.100 (0.5906)	198.030 (88.9595)	-43.580 (30.9306)	-5.631 (4.6047)	0.947 (0.8668)	-4.814 (132.8600)	-2.398 (7.1233)	N.T.	N.T.
Amphibalanus spp. Settlement											
Post-Spat (num. m^{-2} d^{-1})	269.880	4	-4.743 (1.2541)	291.190 (194.8800)	-107.450 (65.6763)	-13.452 (10.0400)	2.733 (1.8404)	1563.100 (290.9400)	-70.742 (15.5281)	N.T.	N.T.
ln[Spat (num. m^{-2} d^{-1})]	1.024	4	-0.008 (0.0150)	0.985 (1.6792)	4.335 (0.7858)	-0.091 (0.0877)	-0.022 (0.0220)	12.106 (0.2099)	-0.649 (0.1357)	N.T.	N.T.
Megabalanus tintinnabulum Settlement											
ln[Post-Spat (num. m^{-2} d^{-1})]	0.570	9	N.I.M.	1.682 (0.2812)	1.404 (0.2658)	N.I.M.	N.I.M.	N.I.M.	N.I.M.	N.T.	N.T.
ln[Spat (num. m^{-2} d^{-1})]	0.006	11	N.I.M.	N.I.M.	N.I.M.	N.I.M.	N.I.M.	N.I.M.	N.I.M.	N.T.	N.T.
Amphibalanus reticulatus Biometrics											
Height (mm d^{-1})	0.099	7	-0.001 (0.0001)	0.044 (0.0040)	-0.008 (0.0040)	N.I.M.	N.I.M.	-0.035 (0.0052)	N.I.M.	N.T.	N.T.
Width (mm d^{-1})	0.092	11	N.I.M.	N.I.M.	N.I.M.	N.I.M.	N.I.M.	N.I.M.	N.I.M.	N.T.	N.T.
ln[Tallness (height/width)]	-0.109	7	-0.015 (0.0020)	0.443 (0.0543)	0.135 (0.0655)	N.I.M.	N.I.M.	-0.356 (0.0750)	N.I.M.	N.T.	N.T.
ln[Total Wet Wt. (mg d^{-1})]	2.160	7	-0.037 (0.0068)	0.496 (0.1834)	-0.767 (0.2237)	N.I.M.	N.I.M.	-0.273 (0.2572)	N.I.M.	N.T.	N.T.
ln[Tissue Wet Wt. (mg d^{-1})]	0.333	7	-0.024 (0.0035)	0.625 (0.1330)	-0.656 (0.1094)	N.I.M.	N.I.M.	-0.925 (0.1820)	N.I.M.	N.T.	N.T.
ln[Tissue/ Total Wet Wt.]	-1.967	7	0.017 (0.0040)	N.I.M.	-0.430 (0.0911)	N.I.M.	N.I.M.	N.I.M.	N.I.M.	0.077 (0.0135)	-0.003 (0.0007)

Fouling accumulation decreased at a rate of -9.8 g m^{-2} d^{-1} km^{-1} at 2m in 2015, -1.2 at 7m in 2015, -7.7 at 2m in 2016, and -2.1 at 7m in 2016. It is possible that the steep linear declines for the 2 m plates reflected the beginning of a curvilinear relationships that would have been apparent if 2 m plates further offshore were not lost.

Cross-shelf barnacle abundances

In total, 24,946 post-spat barnacles and 5,290 spat were found on the settlement plates. *Amphibalanus* spp. was the most abundant post-spat barnacle counted (~93.2%), but *Megabalanus tintinnabulum* (~6.1%), *Balanus trigonus* (~0.3%), and *Amphibalanus improvisus* (~0.2%) were also observed. *A. reticulatus* and *A. amphitrite* were pooled as *Amphibalanus* spp. for counts, but *A. reticulatus* represented > 99.3% (1,328 / 1,337) of dissected *Amphibalanus* spp. that were identified to the species-level.

Amphibalanus spp. spat and post-spat accumulation rates (number m^{-2} day^{-1}) varied across distance from shore, depth, and year, *M. tintinnabulum* post-spat abundance (number m^{-2} day^{-1}) varied across year and depth, but no factors were associated with *M. tintinnabulum* spat abundances (number m^{-2} day^{-1}; Figure 2.4; Table 2.2; Appendix B). The distance-by-depth-by-year interactions for *Amphibalanus* spp. post-spat (Table 2.2; Figure 2.4A) and spat (Table 2.2, Figure 2.4B) indicated that four separate regression lines were needed for each year-by-depth combination of plates. Post-spat accumulation rates (number m^{-2} km^{-1} d^{-1}) were -86.2 at 2m in 2015, -2.0 at 7m in 2015, -18.2 at 2m in 2016, and -4.7 at 7m in 2016. Spat settlement decreased with increased distance to shore by 0.46 times at 2m in 2015, 0.97 times at 7m in 2015, 0.91 times at 2m in 2016, and 0.99 times at 7m in 2016. It is possible that the steep linear declines for post-spat on the 2 m plates reflected the beginning of curvilinear relationships that would have

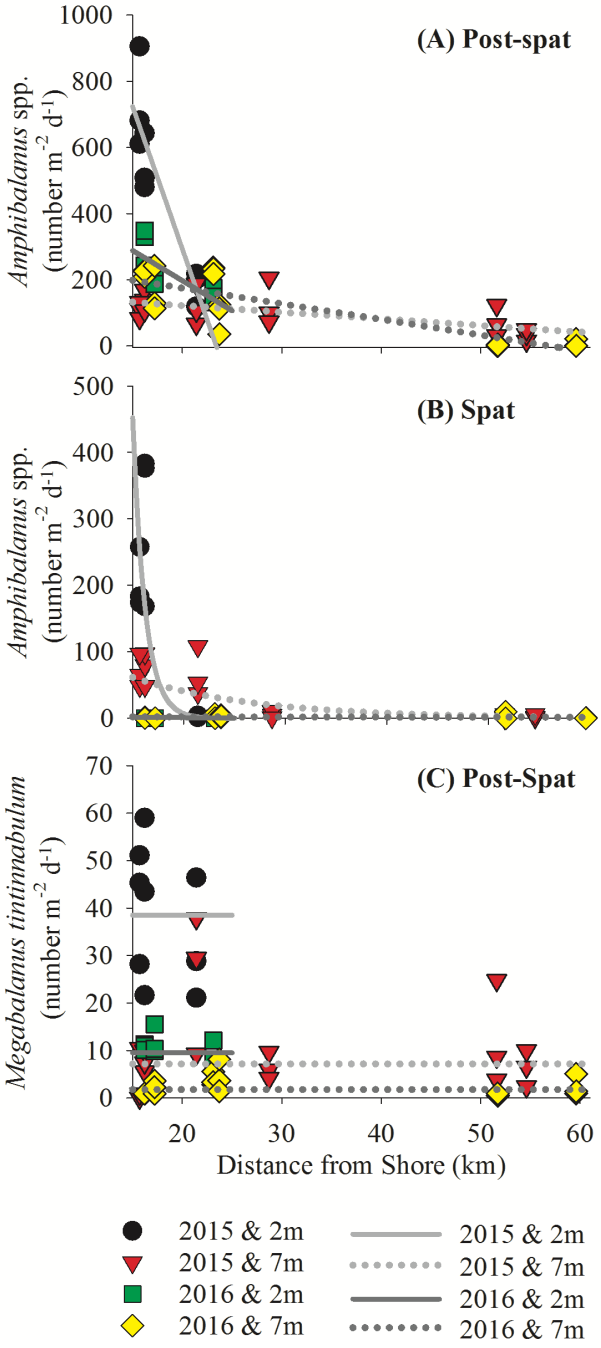

Figure 2.4. Post-spat (A) and spat *Amphibalanus spp.* abundances (B), post-spat and *Megabalanus tintinnabulum* abundances (C) for each year-by-depth combination of settlement plates (2015 & 2m, 2015 & 7m, 2016 & 2m, 2016 & 7m) with varying distance from shore. Regression lines were generated by the GLMM and were plotted for relationships identified as being important by AIC selection. Note the differences in scale for the three y-axes.

been apparent if 2 m plates further offshore were not lost. *M. tintinnabulum* post-spat accumulation rates were not associated with distance but there were generally 4.0 times more post-spat m^{-2} d^{-1} in 2015 vs. 2016 (Table 2.2; Figure 2.4C) and 5.4 times more post-spat m^{-2} d^{-1} at 2 vs. 7m (Table 2.2; Figure 2.4C). None of the variables adequately explained *M. tintinnabulum* spat abundances.

Cross-Shelf Patterns of *A. reticulatus* Biometrics

Biometrics were collected for 1,468 barnacles representing five species; however, analyses were focused on *A. reticulatus* since it represented >90% of barnacles sampled for biometrics. Wet and dry tissue weights were significantly related (Wet= 0.02 + 10.29*Dry; t_{213} =31.5, $p < 0.01$; $r^2 = 0.82$) and percent tissue vs. tallness (height / width) was not significant (t_{10} = -0.1, $p = 0.94$).

A. reticulatus heights (mm d^{-1}) and tallness (height / weight) were generally greater closer to shore, at 2 vs. 7m, and in 2016 vs. 2015, but widths (mm d^{-1}) were not associated with any factors (Figure 2.5; Table 2.2; Appendix B). Heights decreased with distance from shore (slope= -0.001 mm d^{-1} km^{-1}; Table 2.2; Figure 2.5A), but the depth-by-year interaction indicated that the effect of depth was larger in 2016 vs. 2015. The smallest estimated mean height growth rate was 0.02 mm d^{-1} (60 km to shore at 7m in 2015) and the greatest was 0.13 mm d^{-1} (15 km to shore at 2m in 2016). Tallness decreased with distance from shore (Table 2.2; Figure 2.5C), but the depth-by-year interaction indicated that the effect of depth was larger in 2016 vs. 2015. The smallest estimated mean tallness was 0.36 (60 km to shore in 2016 & 7m) and the greatest was 1.11 (15 km to shore, 2016 & 2m).

The total and tissue wet weights (mg d^{-1}) of *A.* reticulatus decreased with increased distance from shore, were greater in 2016 vs. 2015, and were greater at 2 vs. 7m (Figure 2.6;

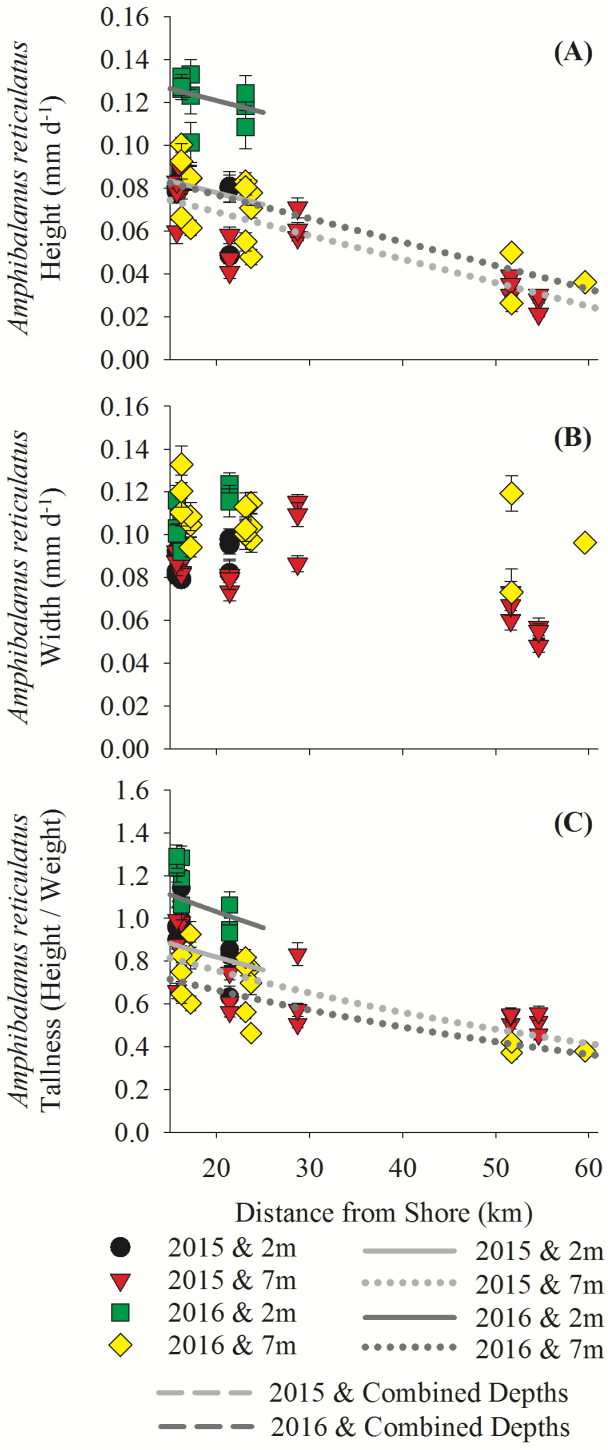

Figure 2.5. *Amphibalanus reticulatus* height (mm day^{-1}; A), width (mm day^{-1}; B), tallness (height/width; C) for each year-by-depth combination of settlement plates (2015 & 2m, 2015 & 7m, 2016 & 2m, 2016 & 7m) with varying distance from shore. Regression lines were generated by the GLMM and were plotted for relationships identified as being important by AIC selection.

Table 2.2; Appendix B). Total weight gain decreased with increased distance from shore (Table 2.2; Figure 2.6A). Total weight gain was generally higher at 2 vs. 7m and in 2016 vs. 2015. But a depth-by-year interaction suggested differences between 2 and 7m were more pronounced in 2016 than 2015 (Table 2.2). The smallest estimated mean total weight gain was 0.43 mg d^{-1} (60 km to shore at 7m in 2015) and greatest was 8.17 mg d^{-1} (15 km to shore, 2016 & 2m). It is notable that the model for total weight gain described here had a similar AIC value as a model

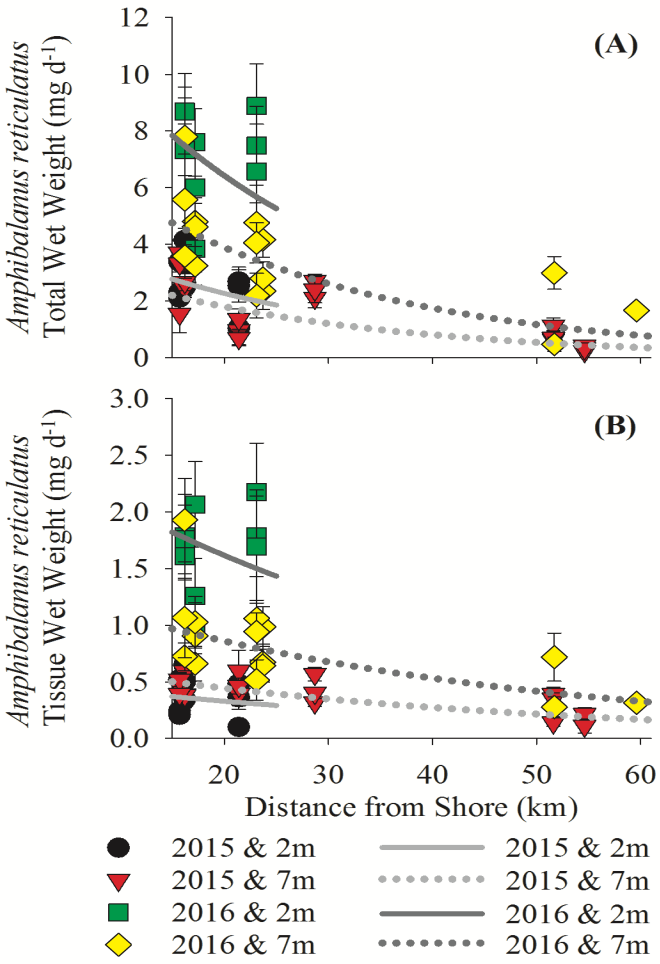

Figure 2.6. *Amphibalanus reticulatus* total wet weight (mg day^{-1}), and tissue wet weight (mg day^{-1}) for each year-by-depth combination of settlement plates (2015 & 2m, 2015 & 7m, 2016 & 2m, 2016 & 7m) with varying distance from shore. Regression lines were generated by the GLMM and were plotted for relationships identified as being important by AIC selection.

that replaced depth-by-year interaction with depth-by-distance (Appendix B). The depth-by-distance model showed increased total weight gain with increased distance to shore at 2m, which was apparently driven by the 2016 data. We chose the depth-by-year model as our final model because regression lines poorly fit the data for the depth-by-distance model. Nevertheless, the plot shows that the relationship with distance from shore at 2m in 2016 was weak and possibly positive. Tissue weights decreased with increased distance from shore (Table 2.2; Figure 2.6B), but the depth-by-year interaction indicated that the magnitude and direction of the depth effect changed across years. The effect of depth was more pronounced in 2016 vs. 2015, and weights were greater at 2 vs. 7m in 2016 and 7 vs. 2m in 2015. The smallest estimated mean tissue weight growth was 0.13 mg d^{-1} (60 km to shore at 2m in 2015) and the greatest was 1.82 mg d^{-1} (15 km to shore at 2m in 2016).

Percent wet tissue of *A. reticulatus* varied across distance from shore, height, and year (Figure 2.7; Table 2.2; Appendix C). Percent tissue was greater in 2016 vs. 2015 (Table 2.2; Figure 2.7). A distance-by-height interaction suggested that percent tissue was similar at all distances from shore for smaller barnacles, but distance had a strong, negative effect for large barnacles and percent tissue peaked at ~25–30%.

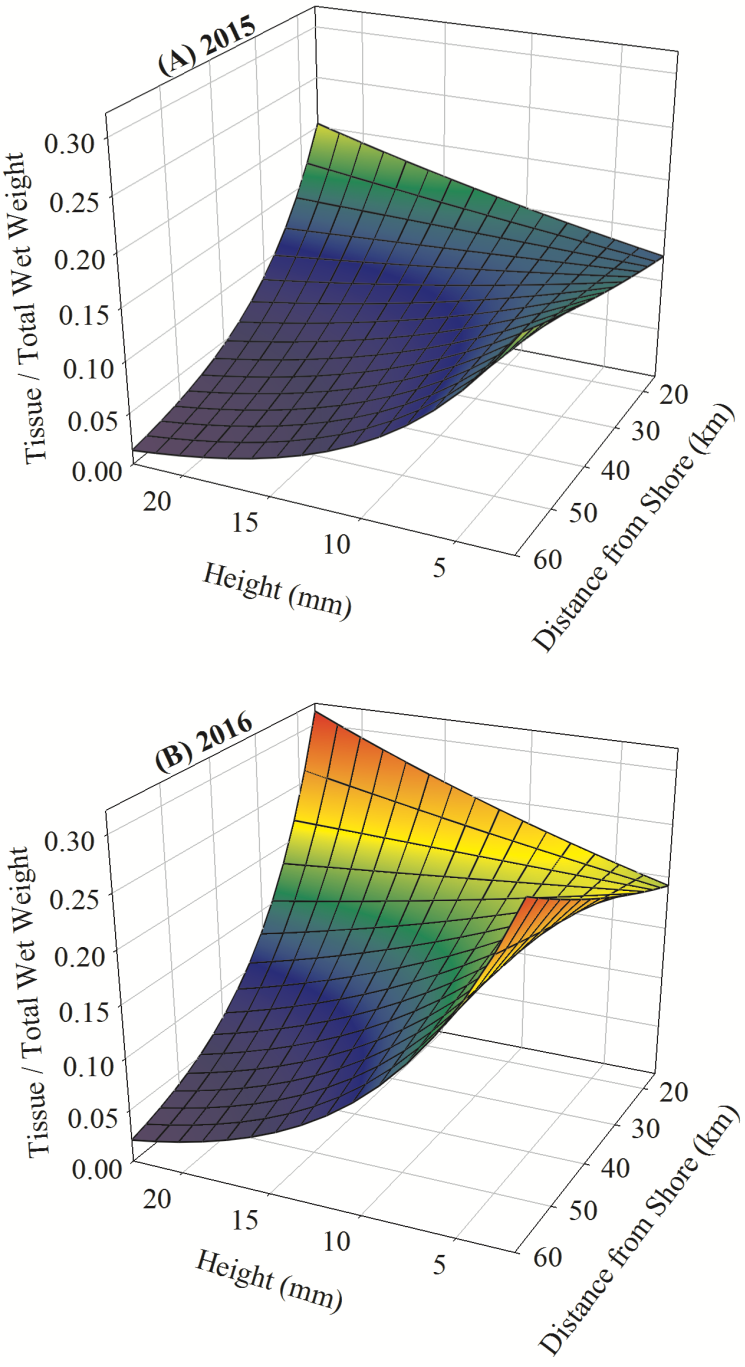

Figure 2.7. Tissue / Total Wet Weight (percent tissue) of *A. reticulatus* across distance from shore and height in 2015 (A) and 2016 (B). Warmer colors correspond to greater percent tissue. The response surfaces were generated by the GLMM.

2.4. Discussion

Fouling accumulation, barnacle settlement, and barnacle growth were markedly higher in nearshore waters where there was prolific primary and secondary production. It is well established that barnacle growth and settlement is greater in areas with higher phytoplankton (Bertness et al. 1991; Menge et al. 2003; Leslie et al. 2005) and zooplankton production (Sanford & Menge 2001). Thus, patterns of productivity probably drove the differences in barnacle settlement and growth described here. Primary and secondary production are generally greater closer to shore and near the surface off Louisiana's coast (Chen et al. 2000). These patterns are driven by discharge from the Mississippi and Atchafalaya rivers (Dortch & Whitledge 1992; Justic et al. 1993; Dagg & Breed 2003), which initially forms a low salinity layer in the surface water that gradually mixes with underlying sea water as distance from shore increases. Low salinity surface waters typically occur within the upper 4 m in Louisiana's nearshore waters (Munnelly 2016; Reeves et al. 2017a, 2017b), where dense phytoplankton blooms are common (Grimes & Finucane 1991; Dortch & Whitledge 1992).

Greater percent tissue (tissue wet weight / total wet weight) of *A. reticulatus* closer to shore and in 2016 vs. 2015 reflects a higher investment in tissue, but this relationship was only apparent for larger barnacles. Percent tissue is often positively related to tallness (height / width) and thus thinner and more brittle shells, but this relationship is species-specific (Wethey 1984) and was not observed here. This is an important consideration since brittle barnacles are more prone to crushing by conspecifics (Connell 1961). Tallness typically increases with barnacle density (Barnes & Powell 1950; Wethey 1984; Bertness 1989), and we found that plates with the highest barnacle settlement and tallness all occurred in the nearshore zone. Higher settlement

and densities of barnacles may create a positive feedback by increasing ease of copulation (Crisp 1976).

Annual variability in the settlement and growth of barnacles may be related to later recruitment of *A. reticulatus* in 2016 than 2015. Highest *Amphibalanus* spp. settlement occurred for the plates at 2 m in 2015, but *A. reticulatus* growth rates were generally higher in 2016 than 2015. This could reflect higher recruitment of *A. reticulatus* in 2015, but it more likely reflects a later recruitment. Barnacles tend to crush and displace their neighbors as they grow outwards in a crowded environment (Crisp 1960; Connell 1961), so settlement may have been similar in 2016 and 2015 but was masked by mortality of some 2016 recruits (see Bertness et al. 1992). Our strongest support for a later recruitment in 2015 was the substantially higher number of *Amphibalanus* spp. spat in 2015. For example, *Amphibalanus* spp. spat settlement at the 2m plates closest to shore in 2015 exceeded 100 spat m^{-2} d^{-1}, but spat were nearly absent in the same area during 2016. Later recruitment in 2015 may have also caused lower estimates of growth rates in 2015 vs. 2016.

Oceanographic features that may influence barnacle settlement and growth

Cross-shelf patterns of temperature and salinity may have influenced barnacle settlement and growth. Temperature is known to be positively related to barnacle growth (Phillips 2005, Inatsuchi et al. 2010), but interaction between temperature and productivity may dampen or intensify their individual effects (Sanford and Menge 2001). In this study, temperature was highest offshore where barnacle settlement and growth were lowest. Cross-shelf differences in plankton productivity may have overwhelmed the effects of temperature. Salinity also tended to increase with distance from shore. Salinity is one of the most important hydrographic features in determining species distributions (Gunter 1961), and it is possible that higher offshore salinity

decreases suitability for *A. reticulatus*. However, we are unaware of research detailing *A. reticulatus* salinity suitability, and it is thus equally likely that higher salinities were more suitable for these barnacles. Barnacles are replaced by sponge and tunicate species as the dominant fouling organisms as distance from shore increases (Lewbel et al. 1987), but sponges and tunicates were not typically found on settlement plates. Barnacles were found on the settlement plates furthest offshore, but their settlement and growth were minimal.

Cross-shelf patterns of total depth and turbulence (wave height) may have also influenced barnacle settlement and growth. The four platforms 15 – 18 km from shore stood in waters with total depths of 7.6 – 8.2 m. Sand was often trapped between barnacles located on the 7m plates at these platforms and barnacles may have benefited from the resuspension of benthic microalgae and organic matter (Oviatt and Nixon 1975; Roman and Tenore 1978a,b). However, the 7m plates at the other eight platforms were > 7m from the bottom, and it was thus unlikely that there was notable influence from the benthos. Consistent declines in growth and settlement at 7m plates across the entire transect and similar trends at 2m plates (all > 5m from the bottom) suggest that the contribution of resuspended organic matter was not a dominant factor. Turbulence also tended to increase with distance from shore, and dislodged the 2m settlement plates at the six platforms furthest offshore (18 plates total). There is often a positive relationship between turbulence and barnacle growth (Crisp 1960; Bertness et al. 1991; Sanford and Menge 2001) and settlement (Bushek 1988; Bertness et al. 1992), presumably because turbulence increases the encounter rate between barnacles and their food supply. However, high turbulence may decrease the ability of barnacles to capture prey by interfering with capture processes (Crisp 1955; Shimeta and Jumars 1991; Eckman and Duggins 1993), which may have contributed to lower barnacle growth offshore.

Currents and proximity to Terrebonne Bay may have influenced patterns of barnacle settlement. There is a strong current off Louisiana's coast that flows longshore (east to west) and dwarfs onshore/offshore transport (Shaw et al. 1985). Shaw et al. (1985) hypothesized that the transfer of fish and invertebrate larvae between bays and the coastal ocean likely occurs during and after the passage of cold fronts when water is advected offshore and then onshore, respectively. If concentrations of barnacle larvae are higher in the bays, proximity of nearshore platforms to Terrebonne Bay may help explain the trend of increased barnacle settlement with decreased distance from shore, given the long larval duration of barnacles (7-13 days for *Amphibalanus eburneus*; Costlow and Bookhout 1957). However, this would not explain cross-shelf differences in growth.

Dominance of nonindigenous species on settlement plates

All barnacles collected during this study are nonindigenous species that are widely distributed. It is well established that shipping is a vector of nonindigenous species (Gollasch 2002; Davidson et al. 2009), but the transit of semisubmersible drilling platforms may pose a greater risk because they support more developed fouling communities than ship hulls (Ferreira et al. 2004). The transit of semisubmersible drilling platforms is known to move entire communities of fishes and invertebrates across biogeographic boundaries (Wanless et al 2010; Yeo et al. 2010), and may contribute to the spread and maintenance of nonindigenous barnacles in the Gulf of Mexico. Platforms in the Gulf of Mexico host many nonindigenous species including orange cup coral (*Tubastraea coccinia*; Sammarco et al. 2004), and lionfish (*Pterois* spp.; Schofield et al. 2017). Given the proximity of platforms to Louisiana's coastal wetlands and the shelf-edge reefs off the Louisiana-Texas coast, it is important to evaluate their potential as vectors of nonindigenous species. In terms of policy, the spread of nonindigenous species

could be a substantial counterweight to ecological services provided by platforms (Page et al. 2006). However, nonindigenous fishes were largely absent from nearshore platforms across coastal Louisiana (Munnelly 2016).

Conclusions: implications for artificial reef management

Higher barnacle settlement and growth in nearshore waters suggests that prolific nearshore primary and secondary production translated to increased production of barnacles at nearshore platforms. The difference between barnacle production at 2 and 7m is striking and supports the argument that the vertical dimension of platforms is an important aspect of their ecological value (Stanley and Wilson 2004; Reeves et al. 2017a; 2017b). Moreover, higher barnacle production at nearshore platforms suggests that nearshore platforms provide a different ecological function than those further offshore, and distance from shore should be considered as a part of artificial reef management plans. These are important considerations since only toppled platforms are considered for inclusion in Louisiana's Artificial Reef Program (Kaiser 2006) and the shallowest platforms currently included in the program are in depths of ~30 m. It should also be noted that barnacle production at platforms is sometimes considered to be less important than primary production (see Daigle et al. 2013). However, without platforms, barnacles would undoubtedly be less common in Louisiana's nearshore waters because there is little naturally occurring hard bottom substrate in this area (Parker et al. 1983). Thus, we consider the production of barnacles and other associated organisms (stone crabs, amphipods etc.) as being a novel and an important characteristic of nearshore fouling communities.

Nearshore barnacle production appears to be an important aspect of the ecological function of platforms because barnacles are prey for commercially and recreationally important species, and they feed on phytoplankton in a region with excessive phytoplankton production.

Gray Triggerfish (*Balistes capriscus*: Gallaway et al. 1981; Beaver et al. 2003; Daigle et al. 2013), Sheepshead (Gallaway et al. 1981; Hoskin and Reed 1984; Sedberry 1987), and Black Drum (*Pogonias cromis*: personal obs.) are known barnacle predators. Stone crabs (*Menippe* spp.) are also known to feed on barnacles (Powell and Gunter 1968; Gallaway et al. 1981) and their abundances are positively associated with living barnacle densities on small platforms (Reeves et al. 2017a). Barnacles are generalist filter feeders that consume a variety of organisms including phytoplankton and zooplankton (Barnes 1959), and may be an important trophic link between phytoplankton and tertiary consumers (Beaver 2002). Barnacle consumption of plankton and the subsequent energy transfer to fish and invertebrate biomass may be especially beneficial to the fishes that prey upon them in coastal Louisiana where the decomposition of plankton leads to the annual formation of the world's second largest hypoxic zone (Turner and Rabalais 1991, 1994; Rabalais et al. 1996). Platform barnacles capture and enhance food web productivity.

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CHAPTER 3: ABUNDANCE AND DISTRIBUTION OF REEF-ASSOCIATED FISHES AROUND SMALL OIL AND GAS PLATFORMS IN THE NORTHERN GULF OF MEXICO'S HYPOXIC ZONE[2]

3.1. Introduction

It is difficult to overstate the economic and ecological importance of Louisiana's coastal zone. The region exports about $152 billion in goods and services annually (Barnes et al. 2015); it holds 40% of the nation's coastal wetlands (Penland et al. 1990) and produced 73.8% of all Gulf of Mexico fisheries landings from 1994–2013 (NMFS, www.st.nmfs.noaa.gov). Louisiana's marine habitats have become substantially modified since the mid-twentieth century. Two of the most dramatic modifications were the installation of massive oil and gas infrastructure (platforms, pipelines) and the development of annually recurring coastal hypoxia (dissolved oxygen <2 mg l^{-1}), which can cause the displacement and/or mortality of marine organisms (Leming and Stunz 1984; Renaud 1986; Craig and Crowder 2001, 2005; Craig et al. 2005; Switzer et al. 2009, 2015; Craig and Bosman 2013).

Oil and gas platforms (platforms) serve as small islands within the northern Gulf of Mexico (nGOM) where fishermen tie up, birds land, and marine biota (algae, invertebrates, fishes, etc.) aggregate, yet continuing debate surrounds the value of platforms as fish habitat (Polovina 1991; Grossman et al. 1997; Gallaway et al. 2009; Shipp and Bortone 2009; Cowan et al. 2011). Platforms are *de facto* artificial reefs that attract large assemblages of fishes (Shinn 1974; Duglas et al. 1979; Harville 1983) and invertebrates (Gunter and Geyer 1955; Gallaway et

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al. 1981; Lewbel et al. 1987; Reeves et al. 2017). Platform infrastructure is collectively considered one of the largest artificial reef systems in the world. It is unclear if platforms increase fisheries production by providing hard bottom substrate, which is otherwise scarce (Stone et al. 1979), or if they only increase harvest by attracting fishes from surrounding areas, making them more exploitable by fisherman (Samples and Sproul 1985; Bohnshack 1989). Past research has largely focused on characterizing platform-associated fauna; however, a few recent studies have explored biomass production potential of platforms with contrasting results (Beaver et al. 2003; Daigle et al. 2013; Claisse et al. 2014).

Abundant fishes and fouling organisms on and around platforms suggest they are important habitats within the nGOM's hypoxic zone. More than 900 platforms occupy Louisiana's nearshore waters (<15 m total depth; BOEM, www.data.boem.gov) that are prone to the development of summer hypoxia. The hypoxic zone typically occupies 15,100–18,000 km^2 off Louisiana's coast (Obenour et al. 2013) and is considered the second largest hypoxic zone in the world (Rabalais et al. 2002). Gulf hypoxia is strongly associated with the bottom and is usually ~3 m thick (Hazen et al. 2009; Reeves 2015). Since platforms span the water column from the sediment to above the surface, platforms may benefit reef-associated organisms by providing hard bottom substrate in the oxygenated waters overlaying hypoxic bottom waters. Hypoxia is believed to alter abundances of some reef-associated fishes and result in their vertical redistribution (Stanley and Wilson 2004), but few studies have focused on how the distributions of reef-associated fishes respond to hypoxia (e.g. Lenihan et al. 2001; Stanley and Wilson 2004).

In this study, we compared abundances and depth distributions of fishes before, during, and after the hypoxia season at groups of platforms subjected to mild and intense hypoxia. Platforms on Ship Shoal (shoal platforms) were subjected to mild hypoxia. Ship Shoal is a

submerged sand shoal located ~15 km south of the Isles Dernieres, LA. This area has previously been used as a reference area for studies evaluating the effects of hypoxia (Baustian et al. 2009; Craig 2012; Craig and Bosman 2013). The shoal is less prone to bottom water hypoxia because its bathymetric relief favors mixing and often precludes stratification (DiMarco et al. 2010; Munnelly 2016). It also supports abundant benthic microalgae populations that produce high oxygen levels when light penetrates to the bottom (Grippo et al. 2009, 2010). In contrast to the surrounding areas, hypoxia on the shoal is intermittent, and when it occurs, mean thickness is ~0.6 m (Reeves 2015). Platforms on the seaward side of the shoal (seaward platforms) experience intense hypoxia that is seasonally persistent and has a ~3.1 m mean thickness (Reeves 2015). We considered mild hypoxia as intermittent and thin compared to intense hypoxia, which is persistent and thicker. Intense hypoxia can be broken up by tropical cyclones (Baustian et al. 2009), but this did not happen during our study.

3.2. Methods

Study Design and Study Area

Fish abundance and hydrographic data were collected at shoal and seaward platforms (Figure 3.1) before, during, and after the hypoxia season, which spanned mid–June to late–August of 2016 (Figure 3.2). Fishes were sampled with a remotely-deployed video array at seven shoal and seven seaward platforms (14 total) on May 31 (before), August 19 (during), and September 11, 2016 (after). Poor visibility precluded our use of video samples at shoal platforms on August 19, 2016. However, we also used the video array to sample fishes at six nearby platforms (three shoal and three seaward; Figure 3.1) as a part of a concurrent study on June 27, 2016. These six samples were included in all statistical analyses to avoid having a missing statistical cell (shoal platforms, during hypoxia).

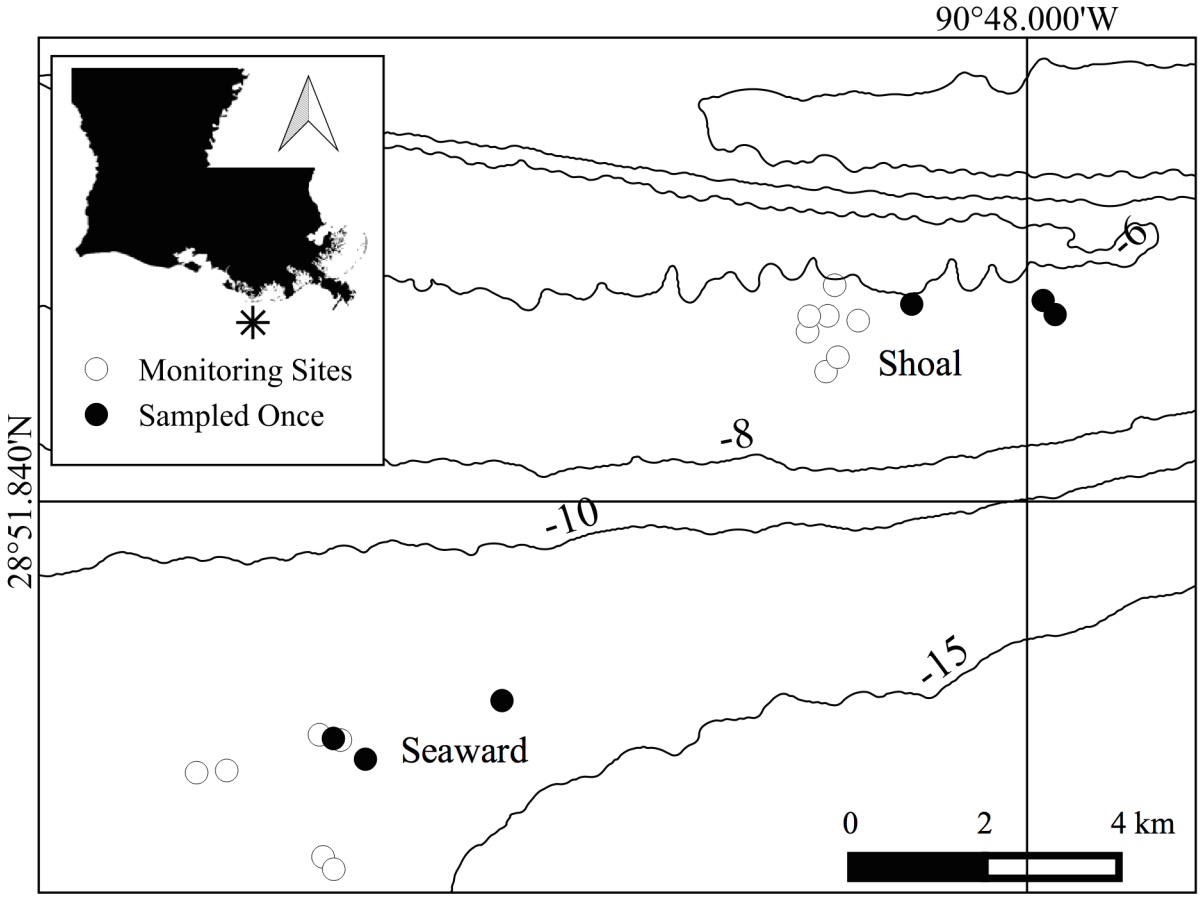

Figure 3.1. Chart of platform locations where fish assemblages were sampled during 2016. White circles denote platforms that were repeatedly sampled and black circles denote platforms that were sampled once on June 27, 2016 as a part of a concurrent study and included in the analyses presented here. The areas considered "shoal" and "seaward" are denoted by the text on the figure.

Seaward platforms were located roughly 7.5–15 km southwest of shoal platforms, and seaward and shoal platforms were located ~24 and 17 km from shore, respectively. Water depths were 14.8±0.52 (mean±SE) at seaward platforms 7.9±0.38 m at shoal platforms (Δ 6.9±0.47 m). Seaward sediment was sandy mud whereas shoal sediment was sand. Platforms used in these analyses were small (≤ 4 pilings with diameters of 4–6 m) and 3 to 44 years old. Sampling efforts focused on small platforms because they were the dominant type of platforms in the study area (>90% of all platforms), they are rapidly being removed (43% reduction since 2006;

BOEM, www.data.boem.gov), and they are not well studied in comparison to larger platforms further offshore. All platforms were active at the time of the study.

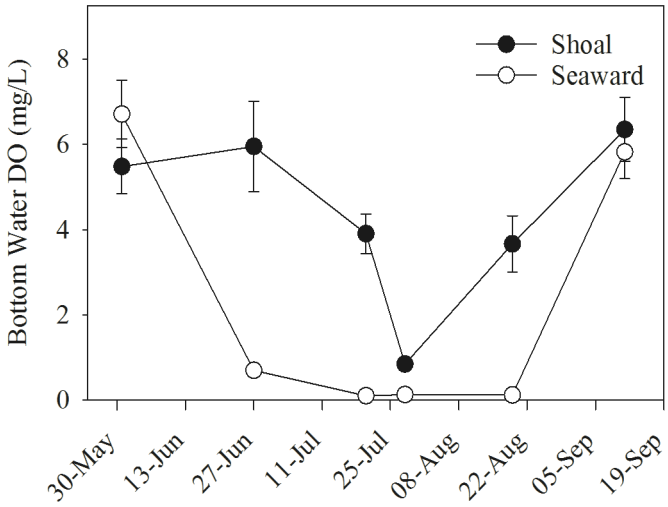

Figure 3.2. Bottom water DO (mg l^{-1}) at shoal and seaward platforms from May 31 to September 11, 2016. Shoal platforms are denoted by black circles and seaward platforms are denoted by white circles. Bottom water DO measurements were taken approximately 0.5 m from the bottom. Error bars denote one standard error of the mean.

Field Sampling

Fish assemblages were sampled using a triangular prism-shaped camera array, consisting of four GoPro™ Hero III video cameras and a depth gauge. Three cameras faced outward, and provided a circular and non-overlapping (62º horizontal/camera) view of the area surrounding the video array. The fourth camera faced downward and provided a view of the depth gauge and bottom substrate. Cameras were synchronized using a GoPro™ Wifi Remote. The array was lowered and raised 3.0 m from the platform at a rate of 0.23±0.02 m/s (95% CI). This method provided a vertical profile of fishes concentrated near the platform.

Hydrographic samples were collected using a YSI 6820 V2 Sonde. The sonde recorded depth (m), dissolved oxygen (mg l^{-1}), salinity (PSU), turbidity (NTU), and temperature (ºC) at

two-second intervals. The sonde was slowly lowered at a rate of 0.04±0.004 m/s (95% CI). The YSI sonde was calibrated before and after each sampling trip using the manufacturer's specifications (YSI Incorporated 2012).

Video-Based Characterization of Fishes

The maximum number of a species (MAXNO) occurring simultaneously in a set of synchronized video frames was used to estimate indices of abundances of all videoed fishes (Ellis and De Martini 1995). MAXNO provides an estimate of abundance and precludes counting the same individual multiple times (Willis and Babcock 2000). For each species, depth of the MAXNO (m) and proximity to the platform were recorded. Proximity to the platform was classified as either being near or away from the platform. MAXNOs near the platform were defined as those where >50% of individuals were between the camera array and the platform (≤3 m away from platform). MAXNOs away from the platform were defined as those where >50% of individuals were recorded by cameras not facing the platform (>3 m away from platform). Water clarity was considered adequate for inclusion of a sample in the analysis when the submerged portion of the platform was visible and in focus. Samples that did not meet these criteria were rejected to avoid biased estimation of species richness and fish assemblage structure. The MAXNO method is widely applied and MAXNOs are referred to by several names including MAX (Willis and Babcock 2000), MIN (Wells and Cowan 2007), MinCount (Bacheler and Shertzer 2015), and MAXN (Bacheler et al. 2013; Schobernd et al. 2014; Campbell et al. 2015). Hereafter, we will refer to MAXNOs as abundances for the sake of clarity, but it should be noted that these are indices of abundance that are specific to the methodology described here.

Species richness and Shannon-Wiener diversity (Diversity) were calculated for each sample. Species richness was estimated as the number of species present at each platform and Diversity was calculated as:

$$\text{Diversity} = -\Sigma_i \rho_i \, log(\rho_i),$$

where ρ_i is the proportion of individuals from the i^{th} species to the total number of individuals present (Shannon 1948).

Statistical Analyses

A factor analysis was used to resolve eight correlated variables into orthogonal factors (Proc Factor; SAS 9.4). The analysis was based on 70 YSI casts, and factors were rotated using the Varimax method. The eight variables used in the factor analysis were upper salinity, bottom salinity, temperature, surface DO, midwater DO, bottom DO, upper turbidity, and bottom turbidity. Upper salinity and turbidity were the means of surface and midwater measurements because surface and midwater salinity and turbidity were highly correlated (Pearson Coefficients> 0.70). Temperature was the mean for surface, midwater, and bottom temperature because of high correlations (Pearson Coefficients>0.57). Factor scores were calculated for each variable and absolute values of loadings> 0.5 were used to characterize factors. Mean factor loadings were plotted for shoal and seaward platforms before, during, and after the hypoxia season to visualize changing environmental conditions.

Principal coordinates analysis (PCO; PRIMER 7; Gower 1966) was also used to visualize patterns of dissimilarity of fish assemblages at shoal and seaward platforms before, during, and after the hypoxia season. The PCO was run on a Bray-Curtis similarity matrix based on the log(abundance+1) of fish species occurring more than five times in the dataset (Bacheler et al. 2013). Principle coordinate loadings were then plotted in bivariate space and a vector overlay

was added to the plot to display the associations of fish species with PCO axes. Fish species were plotted when Pearson correlations were greater than 0.5 and the radii were scaled to the plotted circle of radius 1.0 (perfect correlation).

Generalized linear mixed models (GLMMs) were used to compare patterns of species richness, Diversity, and abundances of the five most common fishes (Gray Snapper *Lutjanus griseus*, Sheepshead *Archosargus probatocephalus*, Atlantic Spadefish *Chaetodipterus faber*, Blue Runner *Caranx crysos*, Atlantic Bumper *Chloroscombrus chrysurus*) across the sampling period (Proc Glimmix; SAS 9.4; Table 3.1). GLMMs included location (shoal and seaward), time (before, during, and after the hypoxia season), and a location-by-time interaction as explanatory variables. Covariates were included to control for variation in platform size (number of pilings) and visibility (midwater turbidity).

Multiple regression analyses were used to examine relationships between species richness, Diversity, and the abundances of the five most common species and hydrography. Multiple regression analyses included Factors 1–3, platform size, and visibility as explanatory variables.

Log-linear models for contingency tables were used to compare the distributions of all species across time, proximity (near vs. away from platform), and depths (Proc Glimmix, SAS 9.4). For each sample, categorizations of where a species' abundance was estimated were used to sort individuals into time-by-depth-by-proximity strata. There were five depth bins at seaward platforms (depths <3 m, 3≥ depths<6 m, 6≥depths<9 m, 9≥depths< 12 m, depths≥12 m), and three depth bins at shoal platforms (depths <3 m, 3≥depths <6 m, depths≥6 m). The response was the number of species in a stratum and was assumed to follow a Poisson distribution using a log-link function. Since there were more depth bins at seaward than shoal platforms (5 vs 3

bins), analyses were performed separately for the two areas. Backward elimination was used to remove interactions and main effects that did not significantly affect goodness-of-fit following Agresti (2007).

All statistical assumptions were met. Since multiple samples were collected at the same platforms, platform names were treated as repeated-measures subjects to account for the clustered structure of the data for all analyses (Nelson 2014). GLMMs and multiple regressions were fitted with either normal, Poisson, or negative binomial distributions based on goodness-of-fit criteria (Shapiro-Wilks, Deviance/d.f.) and residual plots. Atlantic Bumper were not observed during and after the hypoxia season at shoal platforms, so abundances+1 were used to achieve model convergence. A significance level of 0.05 was used for main effects and significance levels for *post-hoc* pairwise comparisons of GLMMs were corrected using Tukey-Kramer adjustments (Day and Quinn 1989). The reported measure of dispersion was one standard error of the mean unless otherwise noted.

3.3. Results

Hydrography

Hydrography varied substantially from the surface to the bottom. DO ranged from 0.1 to 9.6 mg/L and was generally higher at the surface [7.2±0.11 (mean ± SE)] and midwater (6.1±0.15) than the bottom (3.4±0.11). Salinity ranged from 18.2 to 33.6 PSU and was generally higher near the bottom (30.4±0.28) than the upper water column (26.1±0.38). Temperature ranged from 27.0 to 31.0 ºC, but was consistent throughout the water column. Turbidity ranged from 0.7 to 42.2 NTU, and was generally higher near the bottom (6.9±0.93) than the upper water column (2.2±0.17).

Table 3.1. Factor loadings for Factors 1–3, eigenvalues, variance explained by each factor and cumulative variance explained. Factor loading represent the strength and direction of individual variables to each factor, and bold values are those that were used for factor interpretation.

	Factor 1	Factor 2	Factor 3
Upper Salinity	**0.89**	-0.01	-0.12
Upper Turbidity	**-0.79**	-0.30	0.20
Surface DO	-0.33	0.11	-0.14
Bottom Water Salinity	0.27	**-0.69**	-0.44
Bottom Water DO	0.24	**0.94**	-0.01
Temperature	-0.14	0.07	**0.98**
Bottom Water Turbidity	-0.02	-0.13	0.04
Midwater DO	0.11	0.10	-0.01
Eigenvalue	1.68	1.50	1.22
%Variance Explained	21.00	18.75	15.25
%Cumulative Variance Explained	21.00	39.75	55.00

The factor analyses indicated that environmental variation was substantial over space and time. The first six factors had eigenvalues greater than one. We did not interpret Factors 4–6 because only one variable loaded on those factors and they had relatively smaller eigenvalues than Factors 1–3 (1.06–1.09 vs. 1.22–1.68). Factors 1–3 explained 55% of the total environmental variation (Table 3.1). Upper salinity (positive) and upper turbidity (negative) loaded on Factor 1. Factor 1 was characterized as a freshwater influence gradient because low salinity and high turbidity are indicative of freshwater influence. Bottom salinity (negative) and bottom DO (positive) loaded on Factor 2, and thus factor 2 was characterized as being a bottom water oxygen depletion gradient because DO had a strong negative contribution and high bottom salinities were associated with the hypoxic waters below the pycnocline. Temperature (positive) alone loaded on Factor 3. There were pronounced hydrographic differences between shoal and seaward platforms before and during the hypoxia season, but differences were minimal after hypoxia (Figure 3.3). Seaward and shoal platforms exhibited similar changes along Factors 1, 2, and 3 before, during, and after hypoxia. However, the waters surrounding seaward platforms had

greater oxygen depletion than those around shoal platforms during the hypoxia season, experienced less freshwater influence before and during the hypoxia season than shoal platforms, and were warmer before hypoxia and cooler during hypoxia.

Characterization of Fish Assemblages and Patterns of Abundance

There were 29 fish species identified on video representing 16 different families (Table 3.2). Atlantic Spadefish, Sheepshead, Gray Snapper, Blue Runner, and Atlantic Bumper were observed in at least 73% of all samples and constituted 96% of all fishes observed on video. It was impossible to subdivide these five fishes into life history stages based on video. Diver observations indicated that Sheepshead and Atlantic Bumper were adults, Blue Runner were

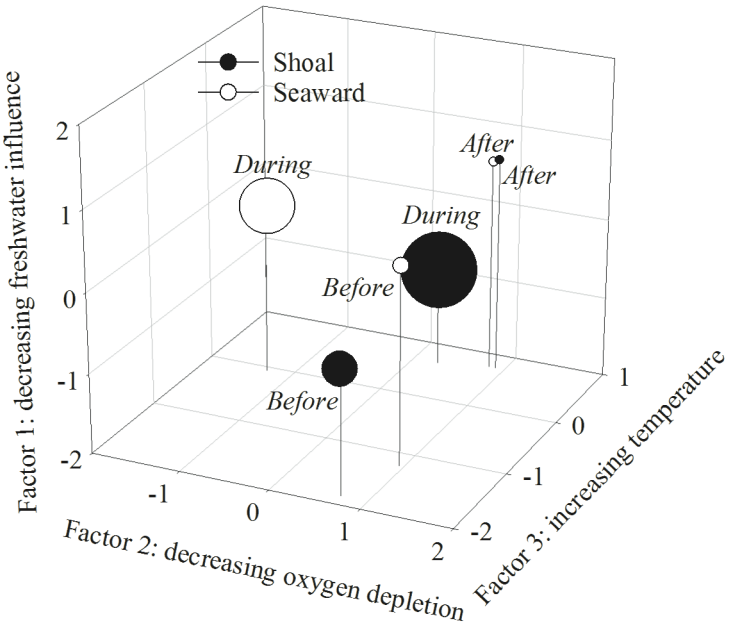

Figure 3.3. Hydrographic factor centroids for shoal and seaward platforms before during and after the hypoxia season. The radii of individual centroids denote two standard errors. Decreasing freshwater influence indicates that upper salinity is increasing and upper turbidity is decreasing. Decreasing oxygen depletion indicates that bottom water DO is increasing and bottom water salinity is decreasing. Increasing temperature indicates that the mean temperature for the entire water column is increasing.

mostly juveniles (age-1), and Atlantic Spadefish were a mixture of adults and juveniles (age-1). Divers also noted that juvenile (age-1) Gray Snapper increased in abundance during the late summer, so Gray Snapper abundances during and after the hypoxia season included both juveniles and adults.

Table 3.2: Frequency of occurrence, mean abundances, and minimum and maximum abundances of each species identified on video. Occurrences represent the percentage of videos where each individual species was present, and SE represents one standard error.

Scientific Name	Common Name	Frequency of Occurrence (%)	Mean (SE) Abundance	Min–Max Abundance
Chaetodipterus faber	Atlantic Spadefish	100	65.0 (5.94)	14–144
Archosargus probatocephalus	Sheepshead	93	13.7 (1.29)	0–35
Lutjanus griseus	Gray Snapper	90	7.2 (0.89)	0–17
Caranx crysos	Blue Runner	85	11.8 (2.06)	0–50
Chloroscombrus chrysurus	Atlantic Bumper	73	382.6 (53.30)	0–1023
Lutjanus campechanus	Red Snapper	65	2.5 (0.55)	0–17
Kyphosus sectatrix	Bermuda Chub	63	1.5 (0.30)	0–8
Caranx latus	Horse-eye Jack	43	1.7 (0.43)	0–11
Pogonias cromis	Black Drum	33	0.7 (0.19)	0–5
Pomatomus saltatrix	Bluefish	30	8.2 (2.87)	0–79
Sciaenops ocellatus	Red Drum	28	0.6 (0.20)	0–7
Elagatis bipinnulata	Rainbow Runner	28	0.5 (0.16)	0–5
Caranx bartholomaei	Yellow Jack	25	1.3 (0.49)	0–16
Abudefduf saxatilis	Sergeant Major	25	1.0 (0.38)	0–12
Caranx hippos	Crevalle Jack	15	0.3 (0.15)	0–5
Balistes capriscus	Gray Triggerfish	13	0.2 (0.07)	0–2
Rachycentron canadum	Cobia	13	0.2 (0.09)	0–2
Trachinotus carolinus	Florida Pompano	10	0.2 (0.12)	0–3
Elops saurus	Ladyfish	8	2.3 (1.96)	0–78
Mugil cephalus	Striped Mullet	5	1.0 (0.69)	0–24
Selene setapinnis	Atlantic Moonfish	5	0.2 (0.16)	0–6
Sphyraena barracuda	Great Barracuda	5	0.1 (0.03)	0–1
Orthopristis chrysoptera	Pigfish	8	0.1 (0.06)	0–2
Lagodon rhomboides	Pinfish	5	0.1 (0.06)	0–2
Aluterus monoceros	Unicorn Filefish	3	<0.1	0–1
Caranx ruber	Bar Jack	3	<0.1	0–1
Dasyatis americana	Southern Stingray	3	<0.1	0–1
Scomberomorus maculatus	Spanish Mackerel	3	<0.1	0–1
Selene vomer	Lookdown	3	<0.1	0–1

The PCO explained 62.2% of total variation in fish assemblages and indicated that fish assemblages differed at shoal and seaward platforms before, during, and after the hypoxia season

(Figure 3.4). There were more Red Drum *Sciaenops ocellatus*, Black Drum *Pogonias cromis*, and Yellow Jack *Caranx bartholomaei* before hypoxia at shoal platforms, and more Gray Triggerfish *Balistes capriscus* at shoal platforms during and after the hypoxia season. Bermuda Chub *Kyphosus sectatrix*, Gray Snapper, Rainbow Runner *Elagatis bipinnulata*, Atlantic Spadefish and Blue Runner abundances increased from May (before) to September (after) across

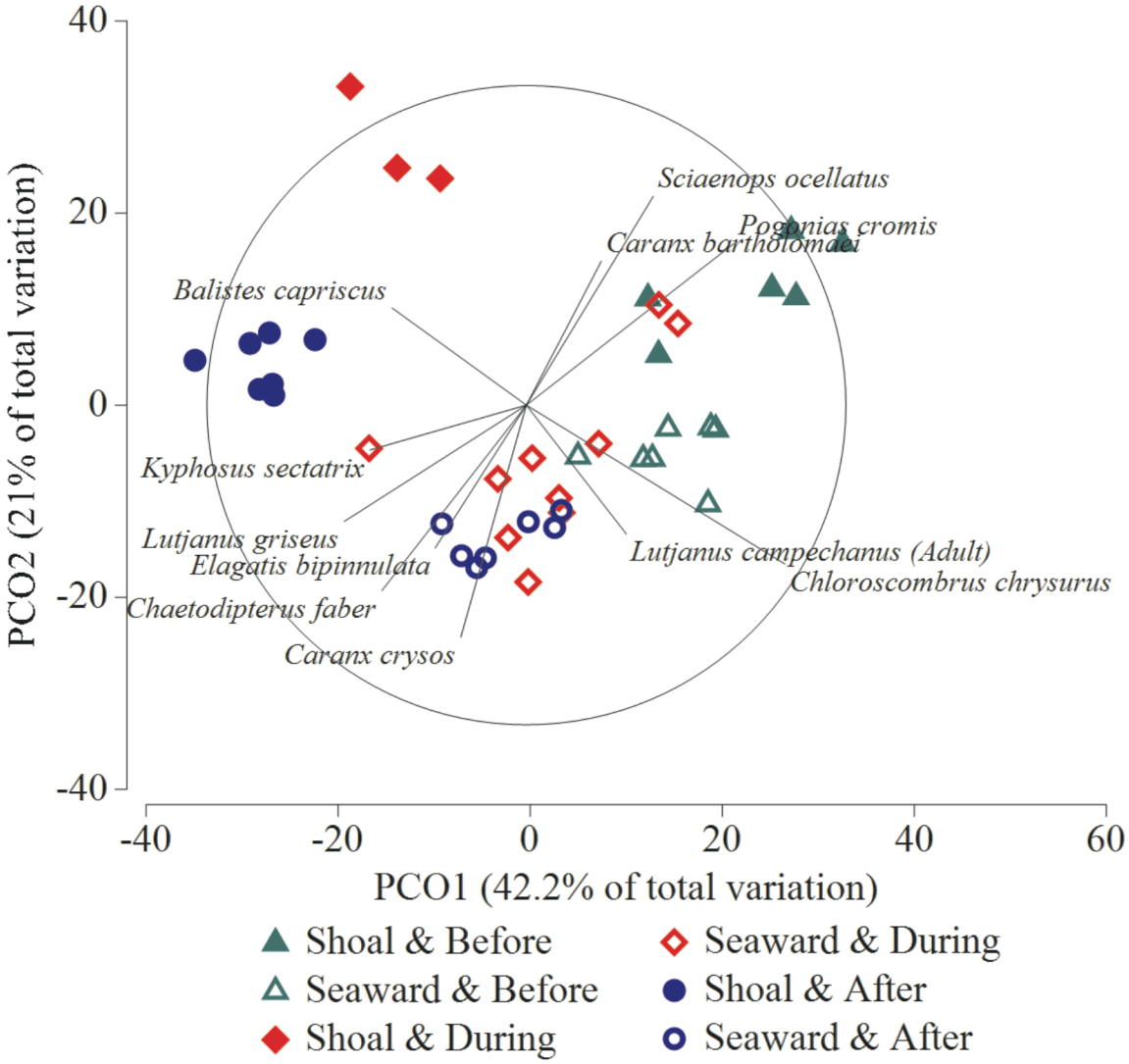

Figure 3.4. Principal coordinate analysis showing the similarity of fish assemblages at shoal and seaward platforms before, during, and after the hypoxia season. Fish species were plotted when Pearson correlations between principal coordinates 1 and 2 were greater than 0.5, and the radii are scaled to the plotted circle of radius 1.0 (perfect correlation).

both locations. Red Drum, Black Drum, and Yellow Jack abundances decreased from May to September across both locations. The PCO showed a divergence of fish assemblages at shoal and seaward platforms during and after hypoxia driven by the disappearance of Atlantic Bumper from shoal platforms before and after the hypoxia season. The shift was not apparent if Atlantic Bumper were removed from the analysis.

Species richness and Diversity generally increased throughout the study period at shoal and seaward platforms, but Diversity diverged at shoal and seaward platforms after the hypoxia season (Figure 3.5A–B; Table 3.3). Species richness significantly increased throughout the

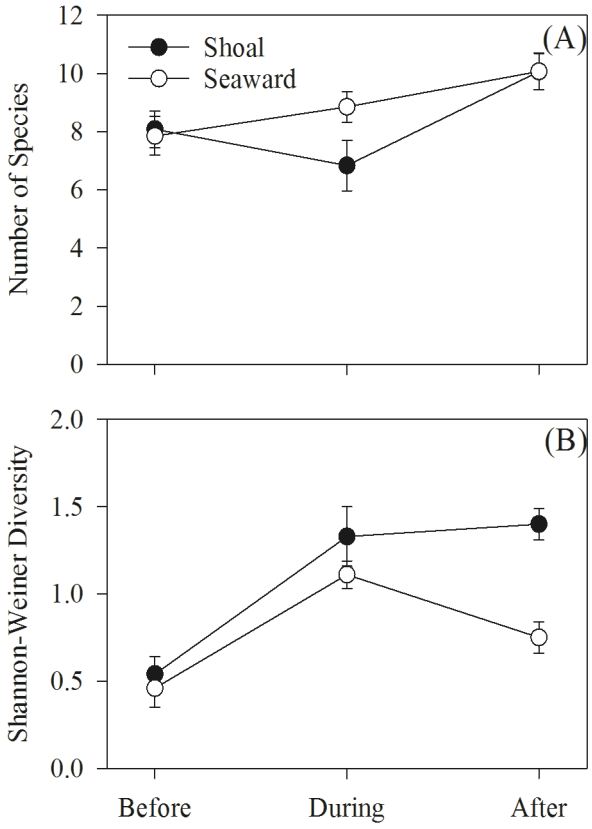

Figure 3.5. Number of species (species richness; A) and Shannon-Weiner Diversity (B) at shoal and seaward platforms before, during, and after the hypoxia season. Black circles denote shoal platforms and white circles denote seaward platforms. Error bars represent one standard error of the mean.

sampling period (P<0.01), but location and the location-by-time interaction were not significant effects (Table 3.3). Diversity increased at both locations before and during the hypoxia season, but a significant location-by-time interaction (P<0.02) indicated that Diversity diverged after the hypoxia season when Diversity was significantly greater at shoal than seaward platforms (*post-hoc* t-test, t= -5.1, P<0.01).

There were differing patterns of abundances for individual fish species across time and locations. Gray Snapper abundance generally increased at shoal platforms and were consistent at seaward platforms, as suggested by a significant location-by-time interaction (P<0.05; Figure 3.6A; Table 3.3). However, Gray Snapper abundance was not significantly different at shoal and seaward platforms after the hypoxia season (t= -2.2, P>0.29). Atlantic Bumper abundance was similar at shoal and seaward platforms before hypoxia, but they diverged thereafter when Atlantic Bumper was absent at shoal platforms and numerous at seaward platforms, as suggested by the significant location-by-time interaction (P<0.01; Figure 3.6E; Table 3.3). Blue Runner abundance was significantly greater at seaward platforms (P<0.01) and significantly varied across time (P<0.02), being greater during and after the hypoxia season than they were before (*post-hoc* t-test, P<0.05). However, there was no significant location-by-time interaction (Figure 3.6D; Table 3.3). Atlantic Spadefish abundance significantly varied across time (P<0.01). They were greater during and after the hypoxia season than they were before (*post-hoc* t-test, P < 0.05), but location and the location-by-time interaction were not significant (Figure 3.6C; Table 3.3). Sheepshead abundance was consistent across the sampling period and the GLMMs indicated that location, time, and their interaction were not significant (Figure 3.6B; Table 3.3).

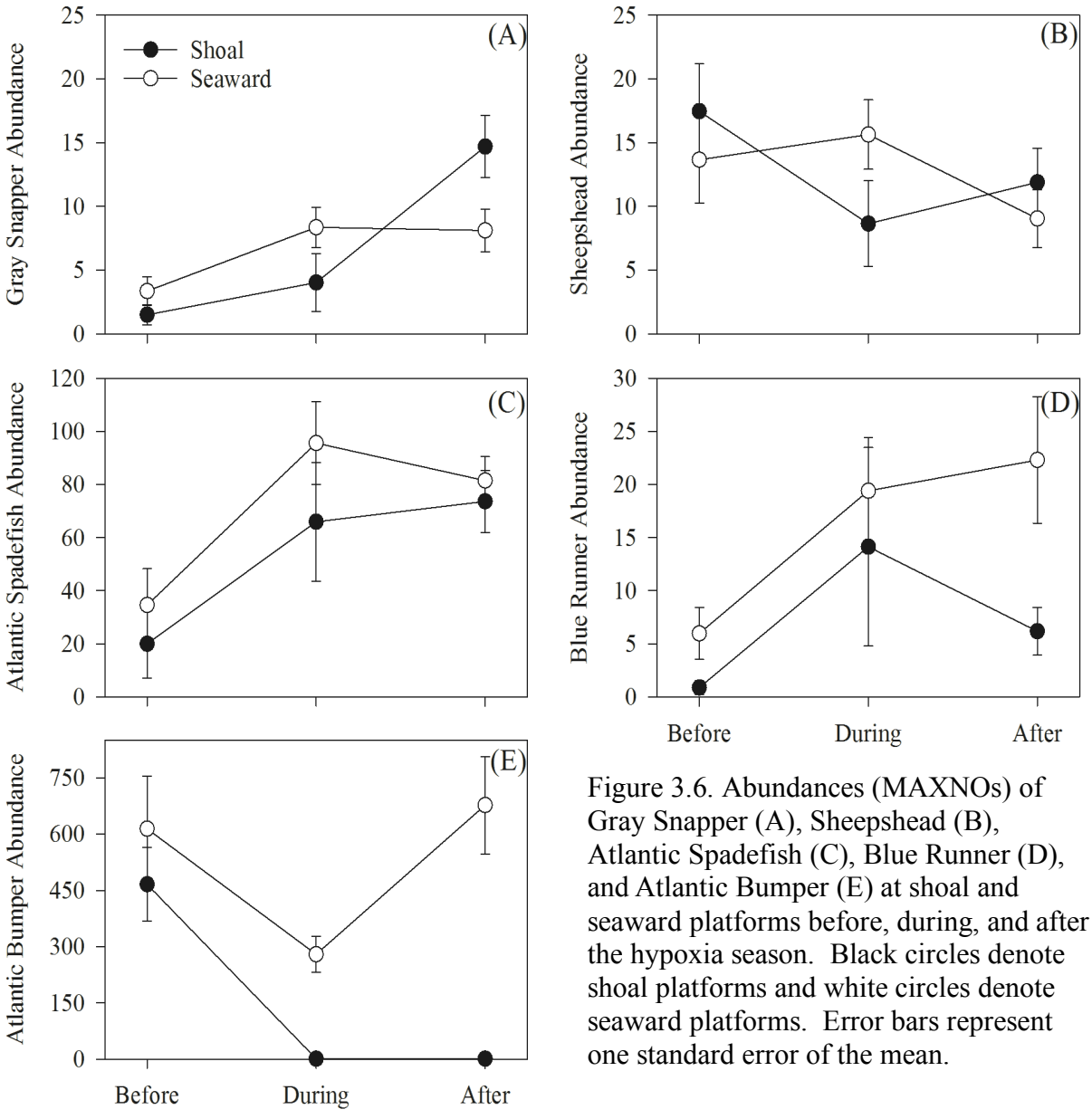

Figure 3.6. Abundances (MAXNOs) of Gray Snapper (A), Sheepshead (B), Atlantic Spadefish (C), Blue Runner (D), and Atlantic Bumper (E) at shoal and seaward platforms before, during, and after the hypoxia season. Black circles denote shoal platforms and white circles denote seaward platforms. Error bars represent one standard error of the mean.

Patterns of species richness and Diversity were associated with the three factors (Factor 1- freshwater influence, Factor 2- bottom water oxygen depletion, Factor 3- temperature), but abundances of individual fishes were mostly unassociated with these factors (Table 3.4). Species richness was negatively associated with decreasing freshwater influence ($P<0.02$), negatively associated with decreasing bottom water oxygen depletion ($P=0.05$), and positively associated with increasing temperature ($P<0.01$). Diversity was positively associated with increasing temperature ($P<0.03$), but there was no significant association between Diversity and the other factors (Table 3.4). Atlantic Spadefish abundance was positively associated with decreasing freshwater influence ($P=0.05$), but there was no significant association with other factors (Table 3.4). Neither Gray Snapper, Sheepshead, Blue Runner, nor Atlantic Bumper were associated with any of the three factors (Table 3.4).

The distribution of fishes changed across depths, proximity to the platform, and time at shoal platforms (Figure 3.7A). The number of species at shoal platforms significantly varied across depth and proximity ($Z=9.5$, $P<0.01$), time and proximity ($Z=3.4$, $P<0.04$) and depth and time ($Z=4.4$, $P<0.01$). The number of species near vs. away from platforms was generally greater at shallower depths than >6 m (0–3 vs. >6 m: $Z=4.0$, $P<0.01$; 3–6 vs. >6 m: $Z=2.4$, $P<0.02$), and there were fewer species near vs. away from platforms after the hypoxia season than before or during (after vs. before: $Z=2.0$, $P<0.05$; after vs. during: $Z=2.3$, $P<0.03$). There were also greater numbers of species at depths of 0–3 m after the hypoxia season than before or during (after vs. before: $Z=3.2$, $P<0.01$; during vs. after: $Z=2.4$, $P<0.02$).

Table 3.4. Slopes, t-values, and *P*-values for the effects of Factors 1–3 on species richness, Shannon-Weiner Diversity, Gray Snapper abundances, Sheepshead abundances, Atlantic Spadefish abundances, Blue Runner abundances, and Atlantic Bumper abundances. Statistics were estimated using multiple regression analysis so slopes, t-values, and *P*-values are partial estimates. Significant *P*-values are denoted with bold text.

Response	**Factor 1**			**Factor 2**			**Factor 3**		
	Slope	*t-value*	*P-value*	*Slope*	*t-value*	*P-value*	*Slope*	*t-value*	*P-value*
Species Richness	-0.31	-2.6	**<0.02**	-0.12	-2.1	**0.05**	0.20	3.3	**<0.01**
Shannon-Weiner Diversity	-0.07	-0.4	>0.71	-0.13	-1.4	>0.19	0.25	2.5	**<0.03**
Gray Snapper	0.75	1.4	>0.17	0.10	0.4	>0.67	0.32	1.4	>0.17
Sheepshead	-0.47	-1.4	>0.16	-0.29	-1.9	>0.07	0.01	0.1	>0.93
Atlantic Spadefish	39.68	2.1	**0.05**	-3.17	-0.4	>0.72	2.27	0.2	>0.81
Blue Runner	0.05	0.1	>0.94	-0.42	-1.2	>0.25	0.68	1.9	>0.07
Atlantic Bumper	-0.22	-0.4	>0.70	-0.05	-0.2	>0.86	-0.06	-0.2	>0.83

Species were not typically observed at depths >12 m when hypoxia was present at seaward platforms, which corresponded with an increase in the number of species occurring at 9–12 m (Figure 3.7C). This was corroborated by the finding of a significant depth-by-time association ($Z=4.4$, $P<0.01$). There were significantly fewer species occurring at depths >12 m during the hypoxia season than before or after (during vs. before: $Z=-2.0$, $P<0.05$; during vs. after: $Z= -1.9$, $P=0.05$), and a significantly greater number of species occurring at depths of 9–12 m during the hypoxia season than before or after (during vs. before: $Z=3.6$, $P<0.01$; during vs. after: $Z=2.3$, $P<0.03$).

3.4. Discussion

Vertical Redistribution of Reef-Associated Fishes

Hypoxia resulted in the vertical redistribution of fishes at platforms with hypoxic bottom waters. Fishes vacated the bottom 3 m of the water column when hypoxia was present at seaward platforms and concentrated in the 9–12 m depth stratum. This reduction to the amount of available space is often referred to as hypoxia-based habitat compression and is consistent with previously reported patterns of fish redistribution, which showed that high densities of fishes occurred in the waters just above hypoxia around platforms (Stanley and Wilson 2004). Vertical redistribution occurred independently of seasonal changes in fish assemblages. Avoidance of hypoxic bottom layers was apparent for all species, including those that were present for the entire summer (Gray Snapper, Red Snapper, Sheepshead etc.) and those that were only present for part of the summer (Red Drum, Black Drum etc.). Avoidance of bottom waters may ultimately limit the amount and type (limited access to sediments) of available habitat and result in some species occupying waters with less-suitable salinity and temperature (Munnelly 2016). Hypoxia-based habitat compression is known to be associated with the vertical

redistribution of organisms in the nGOM (Stanley and Wilson 2004, Hazen et al. 2009; Roman et al. 2012), and it is commonly postulated that this phenomenon increases predator-prey

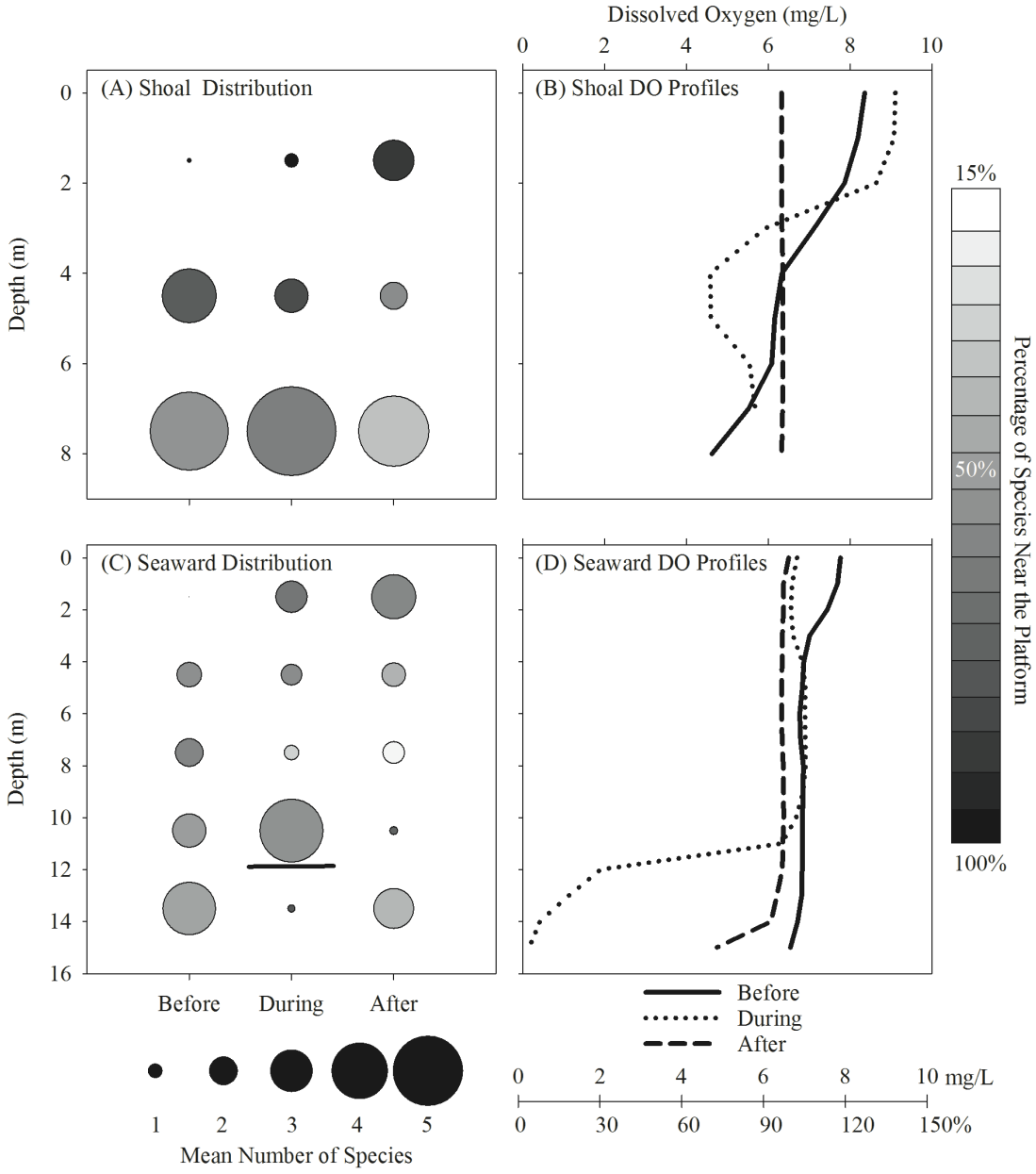

Figure 3.7. Distribution of species and DO profiles at shoal (A&B) and seaward (C&D) platforms before, during, and after hypoxia. Circles represent 3 m depth bins and are scaled to the mean number of species occurring within a bin at shoal or seaward platforms. Color of the circles represents the proportion of abundances occurring near the platform (≤3 m away from platform) for each depth bin. The horizontal bar in plot (C) demarks the vertical extent of hypoxia (DO of 2 mg l^{-1}).

encounters (Breitburg 1994; Eby and Crowder 2002; Eby et al. 2005; Prince and Goodyear 2006, 2007; Hazen et al. 2009; Roman et al. 2012). Crowding could also increase antagonistic behaviors (Aumann et al. 2006) and stress, which may have consequences for reproduction and growth (Bonga 1997; McCormick 2006).

Fishes were also observed to avoid supersaturated ([DO]> 120% saturation) surface waters, which could exacerbate vertical habitat compression and crowding when hypoxia and supersaturation co-occur. Supersaturation appeared to coincide with significantly lower occurrence of fishes at 0–3 m at shoal platforms before and during the hypoxia season. We also observed a lack of fishes in this depth stratum at seaward platforms when supersaturation was present before hypoxia, but there was no significant difference. It is possible that fishes were avoiding lower salinity waters (24.9±0.43 PSU in supersaturated waters vs. 27.4±0.38 in normoxic waters immediately below) or that detection was dampened by higher turbidity since these conditions were typical of supersaturated waters. However, fewer fishes in low-turbidity supersaturated waters suggested that detection alone did not explain lower occurrences of fishes. Fishes are known to avoid supersaturated surface waters around platforms (Munnelly 2016) and extended exposure to supersaturation causes gas bubble disease which is thought to result in fish kills in the nGOM (Renfro 1963). There is obvious coupling between supersaturation and hypoxia because they both result from prolific phytoplankton blooms (Shen et al. 2008; Baustian and Rabalais 2009): the decomposition of phytoplankton near the bottom drives respiration and consumes oxygen, whereas blooms of near the surface result in supersaturated concentrations of oxygen. Nevertheless, the effects of gas supersaturation on fishes in the nearshore zone has not been documented.

The proximity of fishes to platforms did not change in response to hypoxia, but there were differences between shoal and seaward platforms throughout the study period. Fishes were closely associated with platforms in both areas and >55% of species were between the camera array and the platform (≤3 m from the platform). This finding supports the notion that the most fishes are close to platforms (Stanley and Wilson 1998; Boswell et al. 2010). Fishes at seaward platforms were equally positioned on both sides of the camera array throughout the entire water column. This contrasted to shoal platforms where there was decreasing proximity to platforms at greater depths. The primary difference between the two areas was that fishes near the surface on the shoal were more closely associated with the platform, which seemed to be related to the depth distribution of large schools of pelagic fishes (Carangids, Bluefish). Pelagic fishes tended to school away from platforms regardless of the platform's location, and pelagic fishes occurred closer to the bottom at shoal platforms than seaward platforms. This resulted in fishes that are more strongly reef-associated (Atlantic Spadefish, Bermuda Chub, Gray Triggerfish, Sergeant Major) dominating the shallow depths at shoal platforms.

Changes to the Abundances, Species Richness, and Diversity of Platform-Associated Fishes

Patterns of fish abundance at platforms were not driven by the presence or absence of hypoxia. It is well known that reef-associated fishes utilize platforms within the hypoxic zone (Stanley and Wilson 2004), but in this study, the consistency in the composition of the assemblages in areas with different hypoxia intensity was different than what has been previously reported (Stanley and Wilson 2004; Craig and Bosman 2013). Abundances of fishes and Diversity were not associated with oxygen depletion, but GLMMs indicated that Diversity and abundances of Gray Snapper and Atlantic Bumper significantly diverged at shoal and seaward platforms during and after the hypoxia season.

An influx of juvenile Gray Snapper to the shoal drove differences at shoal and seaward platforms after the hypoxia season, but no effect of hypoxia was detected. Gray Snapper abundance was stable at seaward platforms throughout the summer, but they increased by a factor of ten at shoal platforms. Hook and line sampling and diver observations indicated that Gray Snapper present during and after the hypoxia season were mostly juveniles, which were uncommon before hypoxia. Whether the timing and extent of the increased abundance of juvenile Gray Snapper was influenced by hypoxia is unknown, but this species exhibits seasonal ontogenetic movements, with juveniles moving to deeper waters during mid-summer to early fall (Faunce and Serafy 2007; Luo et al. 2009). The Gray Snapper has a benthic diet (Harrigan et al. 1989; Hettler 1989; Franks and Vanderkooy 2000; Yeager et al. 2014), and may aggregate on the shoal because benthic invertebrates are more abundant on the shoal than the surrounding area (Dubois et al. 2009; Gelpi et al. 2009; Reeves et al. 2017). Less intense and more ephemeral hypoxia likely contributes to sustaining greater abundances of benthic invertebrates on the shoal (Dubois et al. 2009; Gelpi et al. 2009) and may indirectly influence Gray Snapper patterns of abundance. Nevertheless, the lack of a significant relationship between Gray Snapper abundance and oxygen depletion may suggest that there was no direct effect of hypoxia.

Atlantic Bumper abundance diverged during and after the hypoxia season when there were no Atlantic Bumper at shoal platforms and many at seaward platforms. The shift in the distribution of Atlantic Bumper also drove divergences for Diversity and fish assemblage similarity, as suggested by the PCO. Atlantic Bumper is commonly found in the hypoxic zone where they move up in the water column to avoid hypoxic bottoms (Hazen et al. 2009; Craig 2012). The absence of Atlantic Bumper at shoal platforms during and after hypoxia contrasts with the earlier finding that Atlantic Bumper is especially common on the shoal when hypoxia is

present in the surrounding area (Craig and Bosman 2013). We are unclear as to why Atlantic Bumper was absent at shoal platforms during and after the hypoxia season.

Seasonal and Locational Differences

Abundances of most fishes changed over the course of the summer, but these changes were probably unrelated to hypoxia. One of the most pronounced changes to platform-associated assemblages was the absence of Black and Red Drum during the late summer. Black and Red Drum were common at shoal and seaward platforms early in the summer and were present on June 27 when hypoxia was well-developed at seaward platforms, but they were not detected later in the summer. As with the changes in Gray Snapper abundances, this was probably associated with seasonal movement patterns since both species are known to migrate from nearshore waters to the bays during the summer (Pearson 1928; Ross et al. 1983) after the cessation of Black Drum spawning (late spring: Nieland and Wilson 1993; Saucier and Baltz 1993) and before the onset of Red Drum spawning (late summer: Wilson and Nieland 1994). Hypoxia can span from late spring to early fall (Rabalais et al. 1991), a period when some fishes are naturally moving in and out of the nearshore zone as water temperature changes. The development and persistence of hypoxia did not seem to interrupt seasonal movement patterns. Thus, it is important that studies evaluating the effects of hypoxia on mobile species account for seasonal changes to distributions by comparing areas of varying hypoxia intensity. A strength of our analysis is that we separated the effects of seasonality and hypoxia by comparing relative changes in areas with varying hypoxia intensity before, during, and after the hypoxia season. This type of study design can be particularly challenging because of the ubiquity of hypoxia in coastal Louisiana. However, oxygenated bottom waters overlaying Louisiana's shoals (Ship, St. Bernard, Tiger,

Trinity, Sabine) create “holes” in the hypoxic zone, and are suitable reference areas for evaluating the effects of hypoxia.

Some differences in the abundances of fishes at shoal and seaward platforms persisted throughout the summer. Blue Runner and Atlantic Spadefish abundances were generally greater at seaward platforms than they were at shoal platforms. The primary difference between the two areas was a 6.9 m difference in depth (seaward: 14.8 m, shoal: 7.9 m). Differences in depth may have played a role in shaping fish abundances because increases in depth co-occur with hydrographic changes (Munnelly 2016) and depth is a significant predictor of fish abundances around platforms (Stanley and Wilson 1991). Nevertheless, species richness, Diversity, and the abundances of many species were similar at shoal and seaward platforms.

Conclusions

Fishes around platforms responded to hypoxia by vertically migrating within the water column, but there was no apparent effect of hypoxia on patterns of abundances and diversity around shallow-water platforms. Platforms may provide refuge for reef-associated fishes living within the nGOM’s hypoxic zone. Platforms span the entire water column providing hard substrate that is utilized by reef-associated organisms in oxygenated waters overlaying hypoxia (Stanley and Wilson 2004; Reeves et al. 2017). This hard substrate is settled by barnacles and other fouling organisms (Gunter and Geyer 1955; Gallaway et al. 1981; Lewbel et al. 1987; Reeves et al. 2017), and undoubtedly provides a source of prey for some species when underlying macrobenthic organisms are decimated by hypoxia (Gaston 1985; Baustian and Rabalais 2009). Because hypoxia occurs during a period when there are strong seasonal shifts in nearshore fish assemblages, reference sites are needed for studies evaluating the effects of hypoxia.

The vertical extent of platforms distinguishes them from traditional artificial reefs (Hernandez et al. 2003; Stanley and Wilson 2004), and is a key aspect of their ecological value in the nGOM. Since shallow-water platforms are quickly being removed, it is important to implement artificial reef management plans that focus on alleviating possible deleterious consequences of losing the unique function that they now provide. Inclusion of standing platforms in Louisiana's Rigs-to-Reefs program would be ideal, but significant maintenance costs and liability associated with standing platforms have precluded their use (Kaiser 2006). Placement of artificial reefs should occur where hypoxia is uncommon or include enough relief to provide refuge above the vertical extent of hypoxia. The relief required to exceed the vertical extent of hypoxia (3–4 m) could still pose a hazard to navigation, but this issue should be explored since platforms in areas with intense hypoxia may provide particularly important benefits to fisherman targeting reef fishes. Furthermore, Louisiana's sandy shoals should be considered as artificial reef planning areas because their propensity to maintain oxygenated bottom waters would enhance the success of lower-relief artificial reefs.

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CHAPTER 4: FORAGING PATTERNS OF FISHES AND THE DISTRIBUTION OF FOULING ORGANISMS AT OIL AND GAS PLATFORMS IN THE NORTHERN GULF OF MEXICO

4.1. Introduction

The northern Gulf of Mexico (nGOM) is home to the world's largest artificial reef (AR) network. Artificial reefs are broadly utilized in coastal oceans with the intention of increasing fisheries productivity and opportunities for anglers (Polovina 1991). A variety of materials are used to construct ARs in the nGOM including fabricated reef modules, concrete bridge rubble, army tanks, and an aircraft carrier. The nGOM is home to >2,000 oil and gas platforms (platforms; BOEM 2017) that are *de facto* ARs (Harville 1983). Platforms host diverse assemblages of fishes (Shinn 1974; Duglas et al. 1979; Harville 1983) and invertebrates (Gunter and Geyer 1955; Gallaway et al. 1981; Lewbel et al. 1987; Reeves et al. 2017b). Platforms span from the seafloor to above the surface. This vertical structure allows barnacles and other fouling organisms to colonize the highly productive surface waters (Reeves et al. 2017b, 2018) where sunlight, nutrients, and plankton are plentiful. Platform superstructures also provide stopover locations for migratory birds, but they may negatively affect birds by inducing nocturnal circulation patterns and resulting in collision-based mortality (Russell 2005).

The ecological importance of ARs in the nGOM has long been debated within the fisheries community. The ecological aspects of platforms have been studied since they were first installed in the nGOM (Gunter and Geyer 1955). However, it is still unclear if ARs create additional fish biomass (e.g. Stone et al. 1979), or if they only attract fishes from the surrounding area (e.g. Samples and Sproul 1985; Bohnsack 1989). Since platforms are removed after their production life ends (Kaiser 2006) and removals are especially high in nearshore waters (total depths < 15.24 m; Pulsipher et al. 2001), it is important to resolve this debate and to determine if loss of these structures needs to be mitigated. Previous nGOM platform studies have primarily

focused on characterizing the abundances and distribution of fishes (Stanley and Wilson 1991, 1997, 1998, 2000, 2004; Boswell et al. 2010; Ajemian et al. 2015; Barker and Cowan 2017; Reeves et al. 2017a) and invertebrates (Gunter and Geyer 1955; Lewbel et al. 1987; Reeves et al. 2017b), and Red Snapper *Lutjanus campechanus* life history (Wilson and Nieland 2001; Nieland and Wilson 2003; Schwartzkopf and Cowan 2016; Glenn et al. 2017; Schwartzkopf et al. 2017). Recent studies have begun to document the magnitude of secondary productivity at platforms (Beaver et al. 2003; Reeves et al. 2018) and to explore platform food webs and energy flow (Daigle et al. 2013; Chapter 4). These studies have expanded our knowledge of the ecological function of platforms, but information gaps remain.

There is a need for more information on the foraging ecology of fishes associated with platforms. Early research documented the feeding ecology of many platform-associated fishes using gut contents analysis (Gallaway et al. 1981), but more recent research has primarily focused on Red Snapper (Simonsen et al. 2015; Foss 2016; Schwartzkopf et al. 2017), and to a lesser degree Gray Triggerfish *Balistes capriscus* (Beaver 2002; Daigle et al. 2013) and Blue Runner *Caranx crysos* (Keenan et al. 2003). A broader understanding of the number of fish species feeding on fouling organisms and the contribution of fouling organisms to fish diets are necessary to determine the ecological value of platforms.

Underwater cameras have revolutionized how fishes are studied in the ocean. Remotely deployed underwater video arrays are broadly employed to monitor fish abundances (Ellis and Demartini 1995; Willis and Babcock 2000; Willis et al. 2000; Cappo et al. 2004; Bacheler et al. 2013; Ajemian et al. 2015; Parker et al. 2016). Underwater cameras have also been used to estimate foraging intensity by deploying cameras to record benthic substrate for extended periods of time and to enumerate feeding activities of fishes (Dunlap and Pawlik 1996; Fox and

Bellwood 2008). The use of underwater cameras to study feeding ecology provides less information about prey type than gut contents, but cameras allow researchers to easily document feeding activities of a variety of fishes and provide a non-lethal sampling method.

In this study, we used a camera array to study the foraging ecology of fishes around platforms in the northern Gulf of Mexico. Platforms were located on Ship Shoal (shoal platforms) and seaward of the shoal (seaward platforms). These two locations experienced different hydrographic conditions over the course of the study. The seafloor surrounding seaward platforms was blanketed by ~3 m of hypoxia (DO < 2 mg l^{-1}) from June to late August/ early September; the seafloor surrounding shoal platforms was typically well-oxygenated, but was briefly blanketed by ~ 1 m of hypoxia in late July (Reeves et al. 2017a). The objectives of this study were to understand 1) how physiochemical, temporal, and biological changes influence fish foraging; 2) the number of different game species foraging on fouling organisms; and 3) the distribution of fouling organisms across space and time.

4.2. Methods

Study area and field sampling

Foraging behavior and fouling organisms were characterized between May 31 and September 11, 2016. Three platforms were sampled on Ship Shoal (shoal platforms) and three were sampled seaward of the shoal (seaward platforms; Figure 4.1). Individual platforms were sampled twice over the course of the study. Seaward platforms were 7.5– 15.5 km southwest of shoal platforms. Seaward platforms were located in total depths of 14.8 ± 0.52 (mean ± SE),

whereas shoal platforms were located in total depths of 7.9 ± 0.38 m. Platforms were small (≤ 2 pilings), which is typical of platforms in the study area (>90%; BOEM 2017).

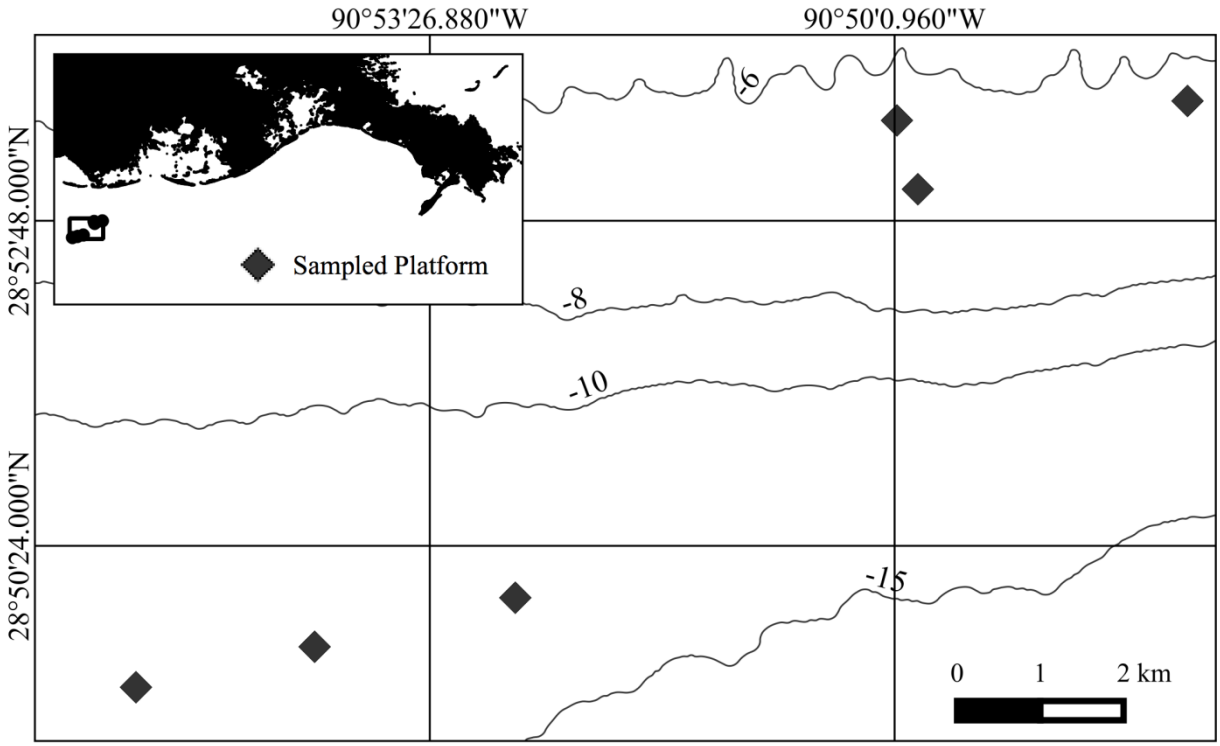

Figure 4.1. Map of the study area. Black diamonds represent platforms where grazing behavior and fouling communities were characterized from May 31 to September 11, 2016. The three platforms in the northeast corner of the map were on Ship Shoal and the three platforms in the southwest corner of the map were located seaward of the shoal. Contour lines denote the depth in meters.

A time lapsed series of photographs recorded foraging of fishes on the upper portion of six small platforms. Cameras were mounted on a 3.0 m long fixed camera array with cameras mounted at 2.0 and 5.0 m of depth (hereafter, referred to as the "SpyCam"; Figure 4.2). GoPro Hero 3 cameras were mounted to both ends of a 3.0 m section of a steel fence pole, which was deployed 3.0 m away from the platform's main piling. Divers confirmed that cameras were facing the main piling and they were set to take one photograph/second. Divers measured the

circumference of the main piling, briefly placed a piece of PVC against the piling to be photographed for scale, and then allowed the SpyCam to record for 1.5-hours.

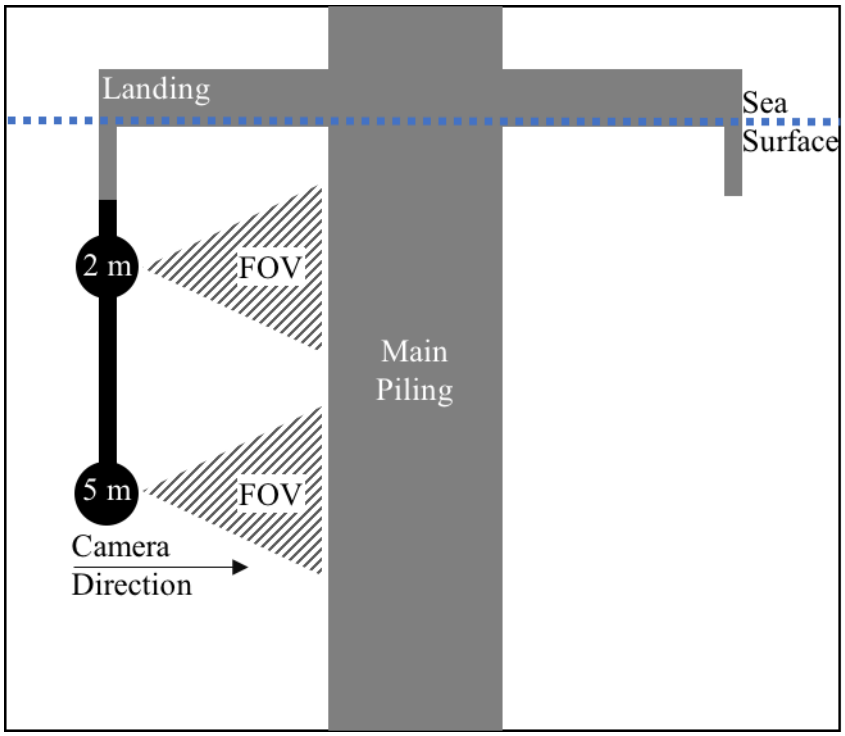

Figure 4.2. Diagram demonstrating how the SpyCam was deployed. Grey areas represent the platform and black areas represent the SpyCam. The two black circles denote the position of each camera. Hatched shading denotes the vertical field of view (FOV) of the cameras. We attempted to mount the camera 3.0 m from the main piling.

The assemblage of fouling organisms was characterized by divers following the 1.5-hour SpyCam deployment. Divers vertically profiled the main piling with a 25-by-25 cm quadrat with an attached GoPro Hero 2 (QuadCam; Reeves et al. 2017b). The QuadCam was placed against the piling at 1.5 m vertical intervals and used to visually estimate density of living barnacles, dead barnacles, algae, and bryozoa following Reeves et al. (2017b). The QuadCam was also used to estimate densities of blennies (Blenniidae) by counting blennies within the quadrat. Stone crabs were counted on the main piling between depths of 2.0 and 7.0 m following Reeves et al. (2017b). Stone crab counts were then converted to densities by dividing the total number of stone crabs by the surface areas surveyed. Since two species of stone crabs were present (Gulf

stone crabs *Menippe adina* and Cuban stone crabs *Menippe nodifrons*), their densities were estimated separately. Divers spent the final 10 minutes of their dives collecting stone crabs and blennies that were located between 2.0 and 7.0 m for biometrics. All collected organisms were identified to the species-level, measured to the nearest mm [carapace width for crabs (CW) and standard length (SL) for blennies], and weighed to the nearest 0.1 g (wet weights). We also recorded the sex of stone crabs.

We estimated abundances of large reef-associated fishes and collected hydrographic data as a part of a concurrent study (Reeves et al. 2017a). Abundances of reef associated fishes were estimated using a four-camera array of GoPro Hero 3 cameras that was lowered from the bow of the boat and hydrographic profiles were collected using a YSI 6820 V2 Sonde. The sonde was lowered from the boat at a rate of 0.04 ± 0.0037 m s^{-1} (95% confidence interval) and measured dissolved oxygen (mg l^{-1}), salinity (PSU), temperature (ºC), turbidity (NTU) every two seconds.

Analysis of SpyCam time lapse samples

The total number of foraging incidents and the total time fishes were foraging during a one-hour interval were estimated from the SpyCam time lapsed photos. The first and last fifteen minutes of time lapses were excluded from analysis to avoid biases associated with diver activities as well as the departure and arrival of the boat. Prior to analysis, photos from the 2.0 and 5.0 m cameras were compared for vertical overlap. When overlap was present, it was removed by cropping photos from both cameras. Next, the surface area photographed was estimated based on the length of the vertical extent photographed and the circumference of the piling. Cropped photographs were then reviewed in time-lapse sequences and foraging characteristics recorded. Fishes were considered to be foraging when their mouths were oriented towards the piling and they were attempting to capture prey by prying and/or pecking at fouling.

Enumerating these foraging incidents required that photographs were viewed in sequence, and the entire series of photographs where an individual fish exhibited this behavior was considered a single foraging incident. The total amount of time (seconds) foraging was enumerated by counting the number of photographic frames where each species was foraging. It should be noted that sometimes multiple fishes from the same species were simultaneously foraging. These cases were considered multiple foraging incidents; however, individual photographs with a fish species simultaneously foraging only counted as one second because the total time spent foraging per species could not exceed one hour per sample. Poor visibility precluded the use of SpyCam photographs from 2.0 m cameras for four deployments and from 2.0 and 5.0 m cameras for one deployment.

Statistical analyses

Assumptions were met for all statistical tests and all tests were run in SAS 9.4. Models that assumed a normal distribution were evaluated with the Shapiro-Wilks test and by examining plots of Student residuals-by-predicted values. Models that were assumed to follow a Poisson distribution were evaluated with deviance/degrees of freedom, and models assumed to follow a binomial distribution were evaluated with the Hosmer-Lemeshow test. Platform names were treated as repeated measures subjects for all analyses to account for the clustered nature of the data (Nelson 2014), and individual platforms were treated as the sampling unit. An alpha of 0.05 was used and the reported measure of dispersion was one standard error unless otherwise noted. *P*-values and test statistics were not reported for models that were selected using information criteria.

Multiple regression was used to compare the number of Sheepshead *Archosargus probatocephalus* foraging incidents (number m^{-2} h^{-1}) and the time Sheepshead spent foraging

(time m^{-2} h^{-1}) across biological, physiochemical/abiotic, and temporal and locational variables (Table 4.1) using generalize linear mixed models (GLMMs). All possible models with one or two variables were compared using Akaike's Information Criteria corrected for small sample sizes (AICc), and the model with the lowest AICc was selected as the final model. Models with similar AICc (Δ AICc < 2) were considered to have comparable fit (Bolker 2008). No more than two variables were included in models because of the limited number of observations (n = 18). Hydrographic variables were measured near the location depth of the cameras; variables measured using the QuadCam represented the means of measurements shallower and deeper than each camera (1.5 and 3 m for the 2.0 m camera and 4.6 and 6.1 m for the 5.0 m camera); and videos used to estimate abundances of large reef-associated fishes were recorded before each SpyCam deployment.

Coverage of living barnacles (%) and blenny densities (count m^{-2}) were compared across time (days since May 31), depth (3 m bins starting at 1.5 m), and location (seaward vs. shoal), and total stone crab densities (Gulf + Cuban stone crab counts m^{-2}) were compared across time and location using GLMMs. Coverage of living barnacles and blenny densities were the means of two quadrats in each 3-m depth bin and stone crab density was the density from 2 – 7 m of depth. Density of living barnacles was assumed to follow a binomial distribution with a logit link, blenny densities were assumed to follow a Poisson distribution with a log link, and stone crab densities were assumed to follow a normal distribution. All possible interactions were considered and non-significant interactions were removed using backward elimination in order of interaction complexity.

Table 4.1. Names, reasons for inclusion in analyses, and supporting citations for variables tested in multiple regression analyses of the number of Sheepshead foraging incidents (number m^{-2} h^{-1}) and the time Sheepshead spent foraging (time m^{-2} h^{-1}).

Variable	**Reason for Inclusion**	**Supporting Citation (if available)**
Biotic Variables		
Algae Coverage (%)	Sheepshead Prey	(Overstreet and Heard 1982)
Bryozoa Coverage (%)	Sheepshead Prey	(Overstreet and Heard 1982; Sedberry 1987)
Live Barnacle Coverage (%)	Sheepshead prey	(Overstreet and Heard 1982; Sedberry 1987)
Sheepshead Abundance (count)	Density of conspecifics may influence foraging	
Stone Crab Density (count m^{-2})	Sheepshead prey	(Overstreet and Heard 1982; Sedberry 1987)
Physiochemical/ Abiotic Variables		
Dissolved Oxygen (mg l^{-1})	Influences habitat suitability	(Munnelly 2016)
Presence of hypoxia on the bottom (DO < 2 mg^{-1})	Influences benthic prey availability	(Baustian and Rabalais 2009)
Salinity (PSU)	Influences habitat suitability	(Munnelly 2016)
Temperature (ºC)	Influences habitat suitability	(Munnelly 2016)
Time to dark (hours)	Influences foraging activity	(Stoner 2004)
Time to slack tide (hours)	Influences foraging activity	(Ferno et al. 1986; Stoner 2004)
Temporal and Locational Variables		
Depth of the camera (2.0 vs 5.0 m)	Fouling community changes with depth	This paper
Geographic location (shoal vs. seaward)	Benthic prey availability differs in these two areas	(Gelpi 2012)
Time (days since May 31)	Seasonality may influence Foraging	(Baustian and Rabalais 2009)

Blenny biometrics were compared across time and location and stone crab biometrics were compared across time, location, and sex. Comparisons of blenny SL and stone crab CW were assumed to follow a normal distribution and comparisons of blenny wet weights (g) and stone crab wet weights (g) were assumed to follow a lognormal distribution using GLMMs. SL

and CW were included as covariates for comparisons of weight. Species identification was included as a random effect for blenny analyses and *Parablennius marmoreus* and *Scartella cristata* were excluded from analyses since only one individual was collected for each species. Cuban stone crabs were excluded from stone crab analyses since they only made up 10.6% of all stone crabs.

4.3. Results

Estimates of Foraging Characteristics

Five different species of large reef associated fishes were observed foraging on fouling attached to the main piling (Table 4.2). The SpyCam photographed a total of 1,174 foraging incidents. Sheepshead was the only species that was consistently observed feeding on the platform biota (88.9% of all samples), followed by Gray Snapper *Lutjanus griseus* (33.3%), Horse-eye Jack *Caranx latus* (16.7%), Atlantic Spadefish *Chaetodipterus faber* (5.6%), and Black Drum *Pogonias cromis* (5.6%). Juvenile Gray Snapper were observed foraging in 41.7% of samples during August and September, but they were not observed foraging in any of the samples from earlier in the summer. Sheepshead foraging behavior lasted 18.9 ± 0.62 seconds. Sheepshead were observed with barnacles in their mouths on nine different occasions. The mean duration of the foraging behavior associated with these occasions was 26.6 ± 16.55 seconds (min = 2 and max = 158 seconds).

Multiple Regression Analyses of Foraging Characteristics

Multiple regression analyses indicated the number Sheepshead foraging incidents (number m^{-2} h^{-1}) and the time Sheepshead spent foraging (time m^{-2} h^{-1}) increased with DO (measured at the depth of cameras) and time to slack tide. The model with the lowest AICc contained DO and time to slack tide for the number foraging incidents (AICc = 103.86; Figure

4.3; Appendix 1) and the time Sheepshead spent foraging (AICc = 186.11; Figure 4.4; Appendix 4.2). Modeled slopes suggested there were fewer foraging incidents (number m^{-2} h^{-1}) as DO decreased (245.4 fewer incidents when DO decreased by 1.0 mg^{-1}) and with the approach of slack tide (78.0 fewer incidents when time to slack tide decreased by 1.0 hour). Modeled slopes also suggested that Sheepshead spent less time foraging (time m^{-2} h^{-1}) as DO decreased (18.9 fewer seconds foraging when DO decreased by 1.0 mg^{-1}) and with the approach of slack tide (4.5 fewer seconds foraging when time to slack tide decreased by 1.0 hour).

Table 4.2. Latin name, common name, total number of foraging incidents, mean time of each foraging behavior (seconds), and percent occurrence of foraging incidents for species photographed while foraging on fouling attached to platforms. Summary statistics are based on 18 samples.

Latin Name	**Common Name**	**Total Number of Foraging Incidents**	**Seconds Spent Foraging (Mean ± SE)**	**Percent Occurrence**
Archosargus probatocephalus	Sheepshead	1,119	18.9 ± 0.62	88.9
Lutjanus griseus	Gray Snapper	51	12.9 ± 1.98	33.3
Caranx latus	Horse-eye Jack	2	14.2 ± 6.10	16.7
Chaetodipterus faber	Atlantic Spadefish	1	4.0	5.6
Pogonias cromis	Black Drum	1	23.3	5.6

Distributions of Fouling Organisms

Barnacle densities varied across depth, time, and location (Figure 4.5); blenny densities varied across depth and location (Figure 4.6); and stone crabs densities between 2 and 7 m were not associated with any of the factors examined. Mean barnacle coverage was 52.4% ± (0.06) and dropped at greater depths, but the effect of depth was more pronounced later in the sampling season (depth-by-time interaction: $Z = 7.65$, $P < 0.006$; Figure 4.5). Barnacle coverage was higher at shoal platforms than it was at seaward platforms for depths ≤5.0, but it was higher at seaward platforms than it was at shoal platforms for depths >5.0 (depth-by-location interaction:

Z = 6.97, $P < 0.009$; Figure 4.5). Mean blenny densities were 13.8 m^{-2} ± (2.99), dropped at greater depths (Z = 11.33, $P < 0.001$; Figure 4.6), and were higher at seaward vs. shoal platforms (Z = 6.04, $P < 0.015$; Figure 4.6). Mean stone crab densities were 2.0 m^{-2} ± (0.30) and were consistent across time ($F_{1,4.8} = 0.01$, $P > 0.920$) and location ($F_{1,7.6} = 0.11$, $P > 0.749$).

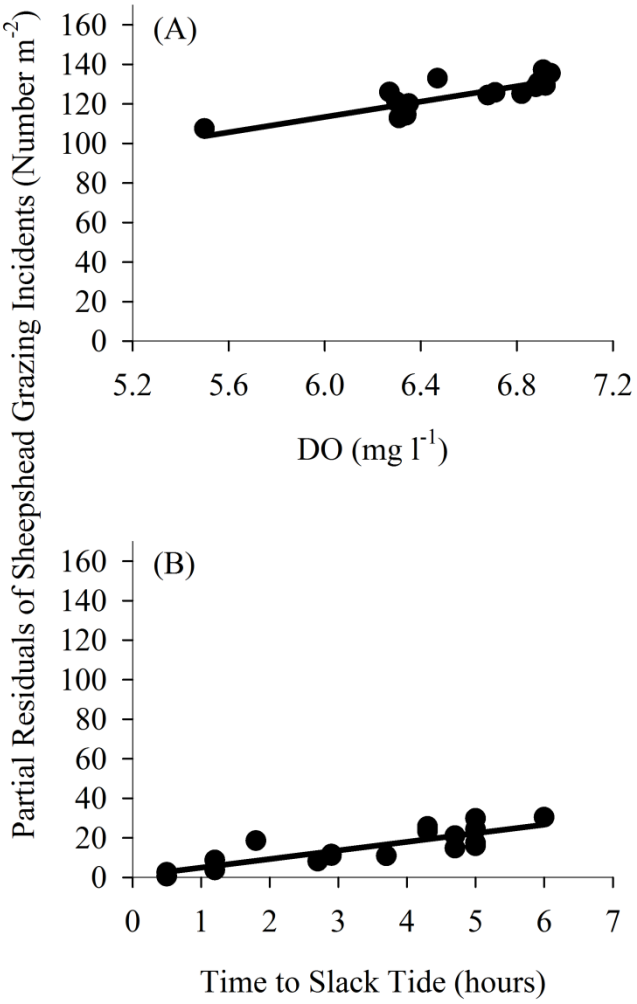

Figure 4.3. Partial residual plots of grazing incidents (number m^{-2} h^{-1}) as a function of DO (mg l^{-1}; A) and time to slack tide (hours; B). Partial residuals and regression plots were generated utilizing multiple regression.

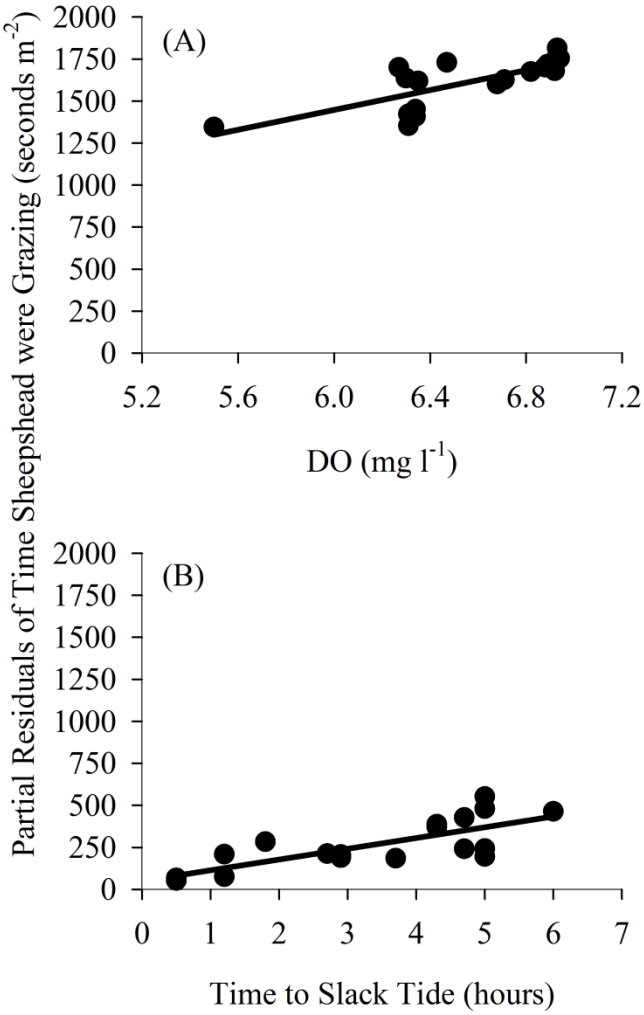

Figure 4.4. Partial residual plots of time Sheepshead were grazing (seconds m^{-2} h^{-1}) as a function of DO (mg l^{-1}; A) and time to slack tide (hours; B). Partial residuals and regression plots were generated utilizing multiple regression.

Biometrics of Fouling Organisms

We collected 161 blennies and 141 stone crabs. There were four species of blennies including 145 Featherduster Blenny *Hypleurochilus multifilis*, 14 Zebratail Blenny *Hypleurochilus caudovittatus*, 1 Seaweed Blenny *Parablennius marmoreus*, and 1 Molly Miller *Scartella cristata*. Mean blenny SL (mm) and weight (g) were 34.4 ± 0.46 and 1.3 ± 0.05,

respectively. There were two species of stone crabs including 126 Gulf stone crabs and 15 Cuban stone crabs. Mean stone crab CW (mm) and weight (g) were 41.3 ± 1.32 and 34.6 ± 3.44, respectively.

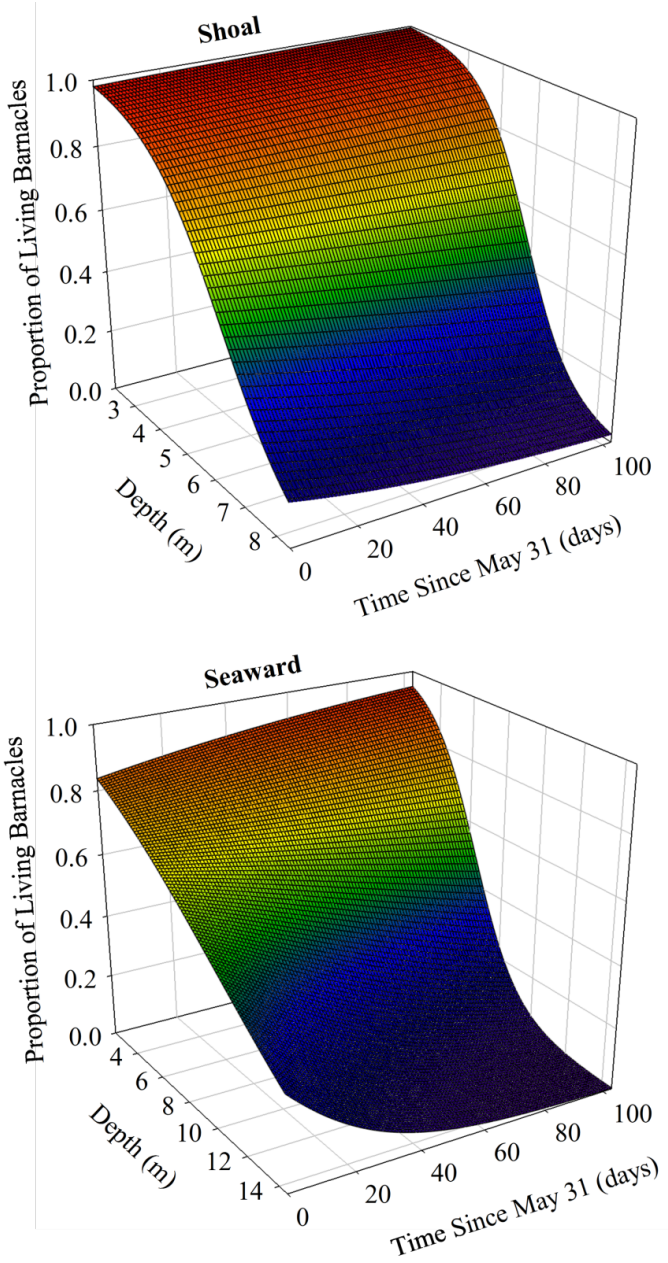

Figure 4.5. Barnacle coverage (% of platform surface covered by barnacles) as a function of depth and time (days since May 31) at shoal and seaward platforms. Response surfaces were generated using GLMMs with a binomial response distribution. Warmer colors correspond to higher barnacle coverage. Barnacle densities were estimated at 3m intervals.

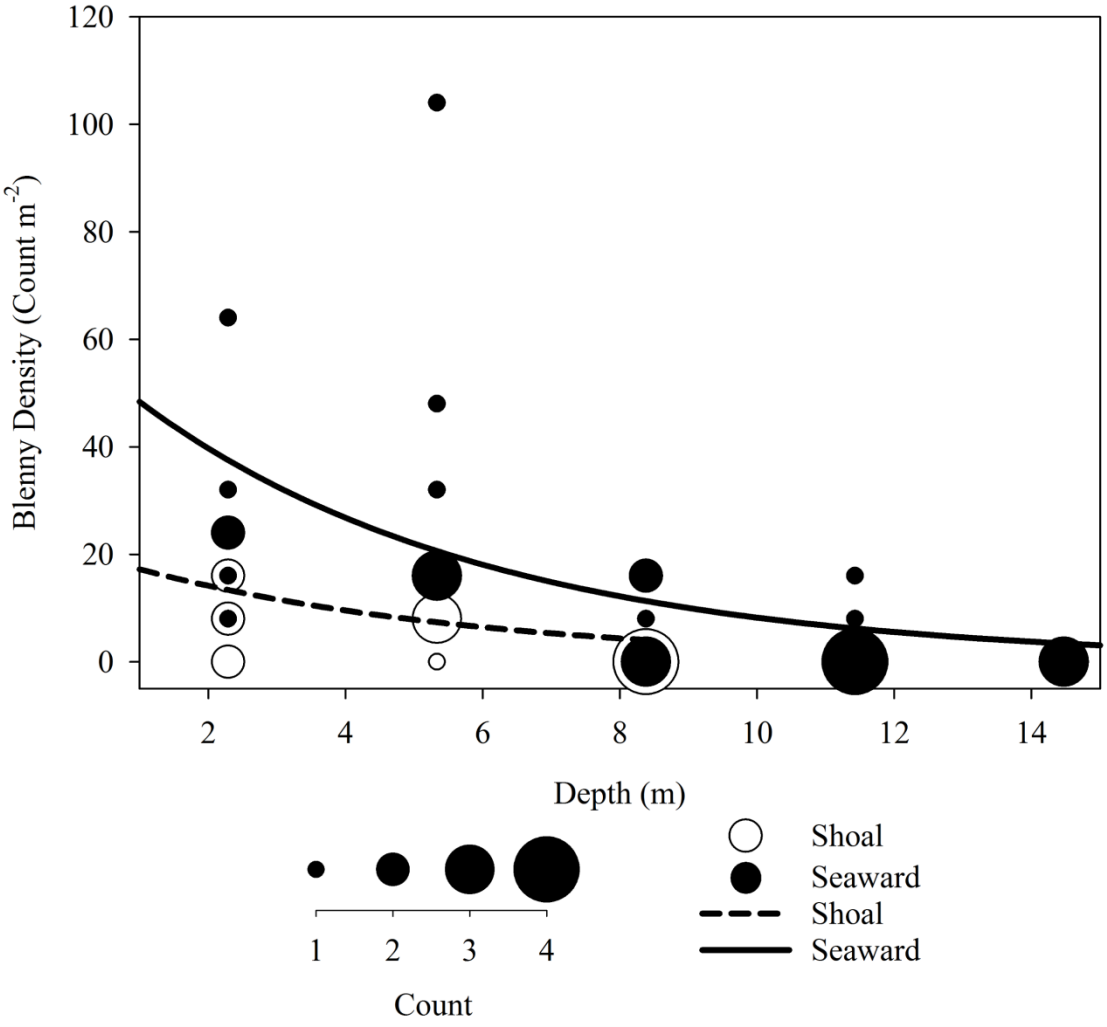

Figure 4.6. Blenny density (number m^{-2}) as a function of depth and location. White circles and the dashed line correspond to blenny densities at shoal platforms, and black circles and the solid line correspond to blenny densities at seaward platforms. Circles are scaled to correspond to the number of measurements with the same blenny densities at shoal and seaward platforms. Regression lines were generated using a GLMM with a Poisson response distribution. Blenny densities were estimated at 3 m intervals.

Blenny biometrics varied across time, stone crab biometrics were not associated with time, depth, or location, and stone crab females tended to be larger than males. Blenny SL significantly decreased late in the summer ($F_{1,157} = 11.85$, $P < 0.001$; Figure 4.7), but did not

vary across locations ($F_{1,3.9} = 0.04$, $P > 0.857$). Blenny weight at size also significantly decreased late in the summer (F1,47.9 = 9.6, $P < 0.006$; Figure 4.8), but did not vary across locations ($F_{1,29.5} = 2.6$, $P > 0.115$). Blenny weight at size was significantly associated with a first order polynomial for SL (SL^2: $F_{1,154.4} = 77.7$, $P < 0.001$). Stone crab CW did not vary across time ($F_{1,112} = 1.2$, $P > 0.272$) or location ($F_{1,4.1} = 0.9$, $P > 0.409$), but females (41.9 ± 4.48) were significantly larger than males (22.1 ± 4.88; $F_{1,120.1} = 15.7$, $P < 0.001$). Stone crab weight at size did not vary across time ($F_{1,188} = 0.08$, $P > 0.774$), location ($F_{1,2.8} = 0.14$, $P > 0.736$), or sex ($F_{1,115.3} = 0.01$, $P > 0.905$). However, stone crab weight at size was significantly associated with a second order polynomial for CW (CW^3: $F_{1,118.9} = 26.7$, $P < 0.001$).

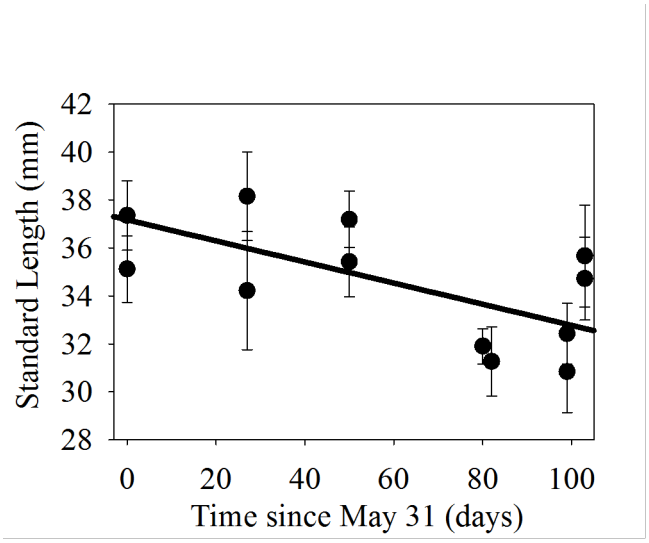

Figure 4.7. Means of blenny standard length (mm) as a function of time (days since May 31). Error bars denote one standard error, and the regression line was generated using a GLMM with a normal response distribution.

4.4. Discussion

Sheepshead foraging patterns were most strongly associated with physiochemical/ abiotic variables, which suggested that prey was not limiting or that the influence of prey availability was dwarfed by other factors. Studies of fish foraging patterns typically use indirect metrics to characterize fish foraging (i.e. gut contents, stable isotopes). Indirect and direct (i.e. video

arrays, diver observations) methods have shown similar trends of foraging activity (Fox and Bellwood 2008), but they provide different insights on foraging. Direct methods can provide new insights on foraging behavior such as strong diurnal patterns (Dunlap and Pawlik 1996), whereas gut contents and stable isotopes provide more specific information on prey composition and energy flow. Examinations of Sheepshead gut contents and stable isotopes showed that they primarily forage on barnacles (Chapter 4). Thus, we suspected that Sheepshead foraging patterns would be associated with barnacle densities; however, DO and time to slack tide better modeled foraging than barnacle densities. It is possible that prey availability is an influential factor, but that it was not more influential than DO and time to slack tide. Indeed, the models with the second lowest AICc values only contained prey as factors (algae and stone crabs for time spent foraging; barnacles and stone crabs for number of foraging incidents). It is also possible that these results were specific to our study area since sampling was conducted in a small region.

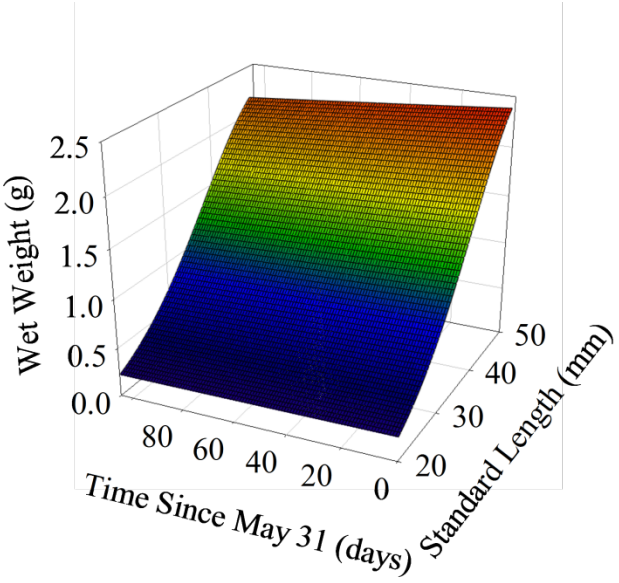

Figure 4.8. Blenny wet weight (g) as a function of time (days since May 31) and standard length (mm). Warmer colors correspond to blennies with greater weights. The response surface was generated using a GLMM with a normal response distribution.

The strong associations between sheepshead foraging patterns and DO and time to slack tide probably reflect the importance of habitat suitability and tidal currents. Sheepshead avoid low oxygen waters, but the lowest values reported in the surface layers where this study took place are well within the range of DO that Sheepshead are known to occupy (Munnelly 2016; Reeves et al. 2017a). The lowest DO saturation level at the depths of camera deployments (~75%) exceeded the 50% threshold where sub lethal effects of DO depletion are thought to occur (Breitburg 2002), and fishes are known to forage in low oxygen waters (Pihl et al. 1992). Nevertheless, depressed levels of oxygen could alter the behavior of Sheepshead since foraging is an energetically demanding activity (Mallekh and Lagardère 2002) and metabolism is reduced in environments with low DO (Fry 1947). Fisherman have long understood that fishes tend to feed at higher rates with increased currents. It is believed that currents carry olfactory stimuli and result in increased foraging (Ferno et al. 1986; Stoner 2004). Barnacle cirral activity is known to increase with higher current velocity (Trager et al. 1990) and it is possible that cirral activity helped Sheepshead locate barnacles.

The two metrics of estimating sheepshead foraging incidents and time spent foraging were highly correlated (*Pearson Correlation Coefficient* = 0.92) and were best modeled by identical variables, but they may have different applications based on the interests of the researcher. One Sheepshead was observed with a barnacle in its mouth after foraging for only two seconds. Since Sheepshead can rapidly capture prey, the total number of foraging incidents may be more informative for studies geared towards understanding consumption. However, total time spent grazing may be better suited for understanding non lethal effects of foraging on prey (i.e. intimidation), which can have similar consequences for prey demographics as direct consumption (Preisser et al. 2005).

Changes to Fouling Organisms

Patterns of barnacle and blenny densities may be directly and indirectly related to hypoxia. Decreased barnacle coverage in the waters near the bottom around late-June was probably related to direct mortality from hypoxia. Persistent hypoxia formed at seaward platforms in late June, and while the shoal's bottom waters were typically oxygenated, hypoxia was briefly present on the shoal in late July (Reeves et al. 2017a). Hypoxia is known to result in the direct mortality of benthic organisms (Sagasti et al. 2001; Baustian et al. 2009; Altieri et al. 2017), including barnacles (Castro et al. 2001; López et al. 2003; Desai and Prakash 2009). Divers noted that the empty barnacle shells in hypoxic waters were extremely brittle, which may be a consequence of decalcification from reduced pH in hypoxic waters (Cai et al. 2011). Brittleness and seasonal mortality of barnacles near the bottom may limit their buildup. Since platform dwelling blennies use barnacle shells for cover (Gunter and Geyer 1955; Gallaway et al. 1981; Rauch 2003; Topolski and Szedlmayer 2004), reduced blenny densities at increased depths may be indirectly related to low DO. However, it is also possible that barnacles are less abundant at depth because barnacle production declines in the lower parts of the photic zone or at depth (Reeves et al. 2018).

Few patterns emerged for stone crab and blenny biometrics, but shifts towards smaller and lighter blennies later in the summer likely reflected an influence of blenny reproduction, recruitment, and/or seasonality. Divers observed many translucent, newly settled blennies on platforms during the late summer. While these blennies were mostly too small to capture or be detected by the QuadCam, some larger juveniles were captured and contributed to the decline in blenny lengths. Fish condition is known to decrease following spawning and can vary seasonally (Le Cren 1951). The observed decline in weight-at-size, shift towards a smaller size distribution,

and presence of newly settled blennies may suggest that the end of the spawning season occurs in the late summer; although we are unaware of research detailing Featherduster or Zebratail Blenny reproduction patterns in the nGOM. Stone crab densities and biometrics did not change across time or location. Reeves et al. (2017b) found a substantial difference between stone crab densities on and off the shoal; however, those samples were collected from a broader geographic area and the off shoal platforms occurred both seaward and landward of the shoal.

Conclusions

The strong influence of time to slack tide on foraging behavior carries broader implications for fisheries sampling. A variety of methods rely on the use of bait to attract fishes, including baited camera arrays (Ellis and Demartini 1995; Gledhill et al. 1996; Willis and Babcock 2000) and more traditional hook-and-line and trap sampling methods. Foraging behavioral patterns is a potential source of bias when relying on bait as a method of attraction (Stoner 2004). However, this potential source of bias could be resolved by including time to slack tide or other measures of current velocity as a covariate in analyses.

This paper provided a new and direct method for estimating foraging at platforms, and showed that only a few fish species persistently foraged on platform-dwelling fauna. Sheepshead were the primary foragers, but observations of Black Drum and juvenile Gray Snapper foraging on fouling organisms were interesting findings. The SpyCam only recorded Black Drum foraging on one occasion, but adult Black Drum captured at shoal platforms in July of 2015 had guts that were filled with barnacles (Figure 4.9). Black Drum are much less abundant at platforms than Sheepshead and juvenile Gray Snapper (Reeves et al. 2017a), which presents a challenge for studying their feeding ecology. However, these observations suggest that fouling organisms associated with platforms may provide a source of prey for Black Drum.

Juvenile Gray Snapper were observed foraging by 41.7% of cameras during August and September. Juvenile Gray Snapper are generalist predators that consume amphipods, shrimp, crabs, and fishes (Franks and Vanderkooy 2000). Juvenile Gray Snapper were uncommon in the study area from May to August, but their abundances increased drastically in August and September (Reeves et al. 2017a). If platforms-dwelling organisms provide a source of prey for juvenile Gray Snapper, it could mark an important ecosystem service because they are a commercially and recreationally important species (commercial landings in the GOM: 131.42 metric tons year^{-1} from 2007-2016; NMFS 2018). Further investigation is needed to understand the foraging ecology of Black Drum and juvenile Gray Snapper around platforms.

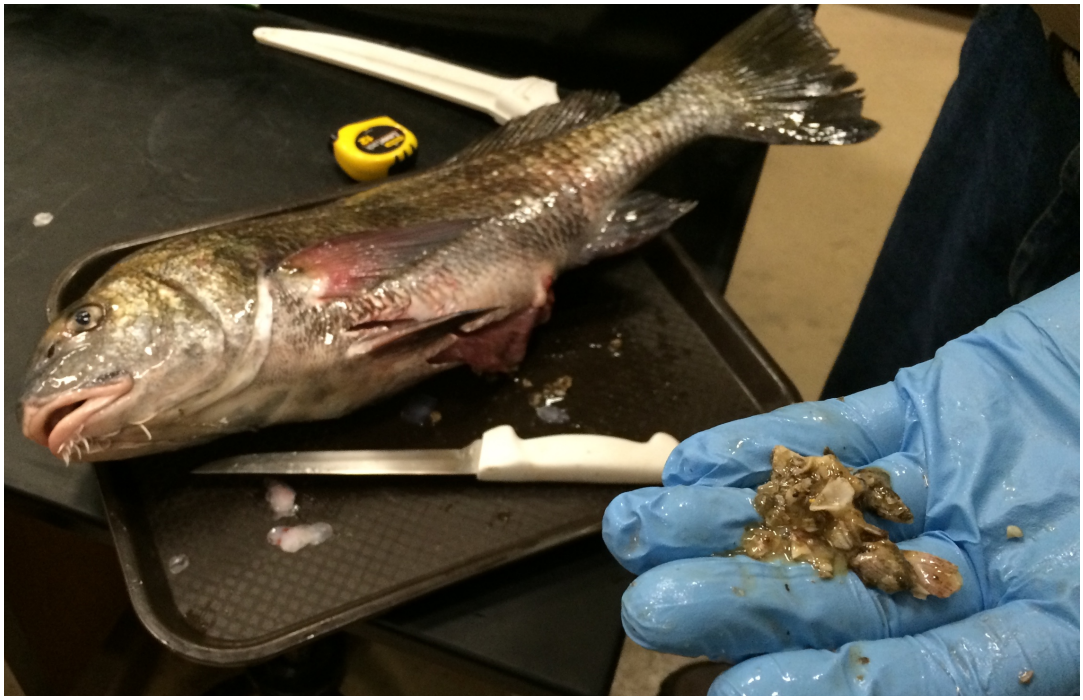

Figure 4.9. Black Drum caught at a shoal platform in July of 2015. Crushed barnacles that were removed from the Black Drum's gut are shown in researcher's hand.

The vertical dimension of platforms allowed fouling communities to persist throughout the hypoxia season. Hypoxia seemed to exert a strong influence over barnacle distributions and likely resulted in barnacle mortality at greater depths. If it were not for the vertical dimension of

platforms, it is unlikely that these communities of fishes and invertebrates would exist within the hypoxic zone. This is an important consideration because commercially and recreationally important fishes (Black Drum *Pogonias cromis*, Gray Snapper, Sheepshead) were observed foraging on platform-dwelling organisms. Moreover, barnacles facilitate the transfer of phytoplankton-produced energy (Reeves et al. 2018) to these species in a region where the die-off of excessive phytoplankton contributes to hypoxia (Turner and Rabalais 1991, 1994; Rabalais et al. 1996).

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CHAPTER 5: SHEEPSHEAD AND STONE CRAB DIETS AT OIL AND GAS PLATFORMS IN THE NORTHERN GULF OF MEXICO

5.1. Introduction

Louisiana's nearshore waters are a sea of paradox. Nutrient discharge from the Mississippi and Atchafalaya rivers fuels prolific primary production (Turner and Rabalais 1991, 1994; Dortch and Whitledge 1992; Rabalais et al. 1996), which results in high fisheries productivity (Gunter 1963). Louisiana accounted for 10.8% of all U.S. commercial fisheries landings by weight from 2006–2015 and was second only to Alaska (NMFS 2017). However, nutrient discharge from the Mississippi and Atchafalaya rivers also leads to the annual formation of coastal hypoxia (DO < 2 mg l^{-1}; Turner and Rabalais 1991, 1994; Turner et al. 2006), which spans 15,100 – 18,000 km^2 (Obenour et al. 2013) and is considered the second largest hypoxic zone in the world (Rabalais et al. 2002). Hypoxia is known to decimate benthic communities (Dauer et al. 1992; Pihl 1994; Baustian and Rabalais 2009) and displace mobile organisms (Leming and Stuntz 1984; Renaud 1986; Craig and Crowder 2001, 2005; Craig et al. 2005; Switzer et al. 2009, 2015; Craig and Bosman 2013). Paradoxically, this region is known as "the Fertile Fisheries Crescent" (Gunter 1963) and "the Dead Zone" (Rabalais et al. 2002).

The nGOM's hypoxic zone is often perceived as a homogenous area blanketed by hypoxia, but it is a dynamic area dotted with sand shoals and oil and gas platforms (platforms) that may provide refuge from hypoxia. Ship, Tiger, and Trinity shoals are within the area affected by hypoxia, but they tend to maintain oxygenated bottom waters when surrounding areas are hypoxic (Dubois et al. 2009; Gelpi et al. 2009; DiMarco et al. 2010; Craig and Bosman 2013; Munnelly 2016). These sand shoals may provide refuge from hypoxia for macrobenthic organisms (Dubois et al. 2009), blue crabs (Gelpi et al. 2009), and fishes (Craig and Bosman 2013; Reeves 2015; Munnelly 2016). There are also ~ 900 oil and gas platforms within the

nearshore waters (< 15 m of water; BOEM 2015) where hypoxia occurs. Since platforms span from the seafloor to above the water surface, they provide hard bottom substrate in the oxygenated waters overlaying hypoxia. This substrate is colonized by barnacles and other organisms that develop diverse fouling communities (Gunter and Geyer 1955; Gallaway et al. 1981; Lewbel et al. 1987). Platforms in the hypoxic zone are known to support high abundances of stone crabs (Reeves et al. 2017b) and reef-associated fishes (Stanley and Wilson 2004; Reeves et al. 2017a), but little is known about the consequences of hypoxia for reef-associated organisms living on and around platforms.

Platforms on Louisiana's continental shelf are *de facto* artificial reefs that attract high abundances of fishes (Shinn 1974; Duglas et al. 1979; Harville 1983; Stanley and Wilson 1991, 1997), but there is ongoing debate regarding their values as fish habitat. There is little naturally-occurring hard bottom habitat in the north-central GOM (2,571 km^2 or 3% of substrate on the Continental Shelf from Pensacola, FL to Pass Cavallo, TX; Parker et al. 1983) and platforms account for an additional ~12 km^2 of hard bottom substrate (Gallaway et al. 1998). The addition of artificial reefs may benefit populations that are limited by hard bottom substrate (Stone et al. 1979), but they may also reduce populations by aggregating fishes and making them more susceptible to fishing (Samples and Sproul 1985; Bohnsack 1989). Debate over these two ideas has continued since their inception (Polovina 1991; Grossman et al. 1997; Gallaway et al. 2009; Shipp and Bortone 2009; Cowan et al. 2011) and is often referred to as the attraction vs. production debate. While the debate is often approached as only having two possible answers (artificial reefs attract or produce fish biomass), there is a spectrum of possibilities between complete attraction or production (Bohnsack 1989) and outcomes along this spectrum are undoubtedly species and location-specific. Understanding biological productivity and how

artificial reefs function in different environmental conditions is key to resolving the attraction vs. production debate (Bortone 1998), and is receiving increased attention.

In this study, we compared the feeding ecology of two reef-associated species, Sheepshead *Archosargus probatocephalus* and Gulf stone crabs *Menippe adina*, during the early and late summer at platforms that experienced mild and intense hypoxia. We hypothesized that reef-associated organisms experiencing intense hypoxia would transition from bottom to platform-dwelling prey over the course of the summer, but those experiencing mild hypoxia would maintain consistent diets. Platforms were located on Ship Shoal (shoal platforms) and seaward of the shoal (seaward platforms) where they experienced mild and intense hypoxia, respectively. The bottom surrounding seaward platforms was blanketed by ~3 m of hypoxia (DO < 2 mg l^{-1}) from June to late August/ early September; whereas, the bottom surrounding shoal platforms was typically well-oxygenated, but was briefly blanketed by ~ 1 m of hypoxia in late July (Reeves et al. 2017a). We compared diets of Sheepshead and stone crabs during the early and late summer at platforms with mild (shoal platforms) and intense hypoxia (seaward platforms) using a combination of stable isotopes, $\delta^{13}C$, $\delta^{15}N$, and gut contents analyses.

Sheepshead and stone crabs were studied because they are abundant at shoal and seaward platforms throughout the summer (Reeves et al. 2017a, 2017b). Benthic invertebrates, including sessile and mobile organisms, are the most common prey of Sheepshead (Gallaway et al. 1981; Overstreet and Heard 1982; Sedberry 1987) and stone crabs (Bender 1971), and Sheepshead are known to forage on platform-dwelling prey (Chapter 3). Both species support commercial fisheries in the Gulf of Mexico, and mean annual landings from 2006 – 2015 were 601 metric tons for Sheepshead and 2,112 metric tons of stone crab claws (*Menippe adina* + *Menippe mercenaria*); however, these organisms are not typically fished at platforms. While 73% of Gulf

of Mexico Sheepshead were landed in Louisiana, only 0.04% of stone crabs were landed in Louisiana (99.7% landed in Florida, NMFS 2017). Sheepshead in the nGOM can live up to 20 years (Beckman et al. 1991) and spawn from February to April (Render and Wilson 1992). Stone crabs can live up to 8 years (Gerhart and Bert 2008) and spawn from April to May (Wilber 1989). Cuban stone crabs *Menippe nodifrons* and Gulf stone crabs are both found at shoal and seaward platforms (Reeves et al. 2017b), but this study focused on Gulf stone crabs.

5.2. Methods

Study Area and Field Sampling

Samples were collected for stable isotope and gut contents analyses during the early (May 31 – July 20) and late summer of 2016 (August 19 – September 11) at shoal and seaward platforms (Figure 5.1; Table 5.1). Broad time categories were used for the early and late summer because the benthos is not significantly affected until roughly one month after the development of hypoxia (Baustian and Rabalais 2009), and hypoxia formed during June in our study area (Reeves et al. 2017a). Seaward platforms were 7.5 – 15.5 km southwest of shoal platforms, and water depths were 14.8 ± 0.52 (mean ± SE) at seaward and 7.9 ± 0.38 m at shoal platforms. Sampling efforts focused on small platforms (≤ 4 pilings) because they represent > 90% of all platforms in the study area (BOEM 2015).

Sheepshead, stone crabs (*Menippe adina*), barnacles (*Amphibalanus* spp.), platform associated macro algae, and sediment were collected from 14 platforms. Sheepshead were collected at platforms adjacent to those where stone crabs, barnacles, algae, and sediment were collected to avoid biasing concurrent studies of Sheepshead abundances and grazing behaviors. Sheepshead were collected using hook and line sampling and spears, Stone crabs, barnacles, and macro algae were collected from the platform's main piling, and divers skimmed surface

sediment from the bottom ~ 4.0 m away from the platform. Sheepshead were measured [mm fork length (FL)] and weighed (g), and guts were extracted. Stone crabs were measured [mm carapace width (CW)] and weighed (g). Sheepshead, barnacles, stone crabs, macro algae, and sediment were frozen at ~ –18ºC and Sheepshead guts were preserved in 10% formalin.

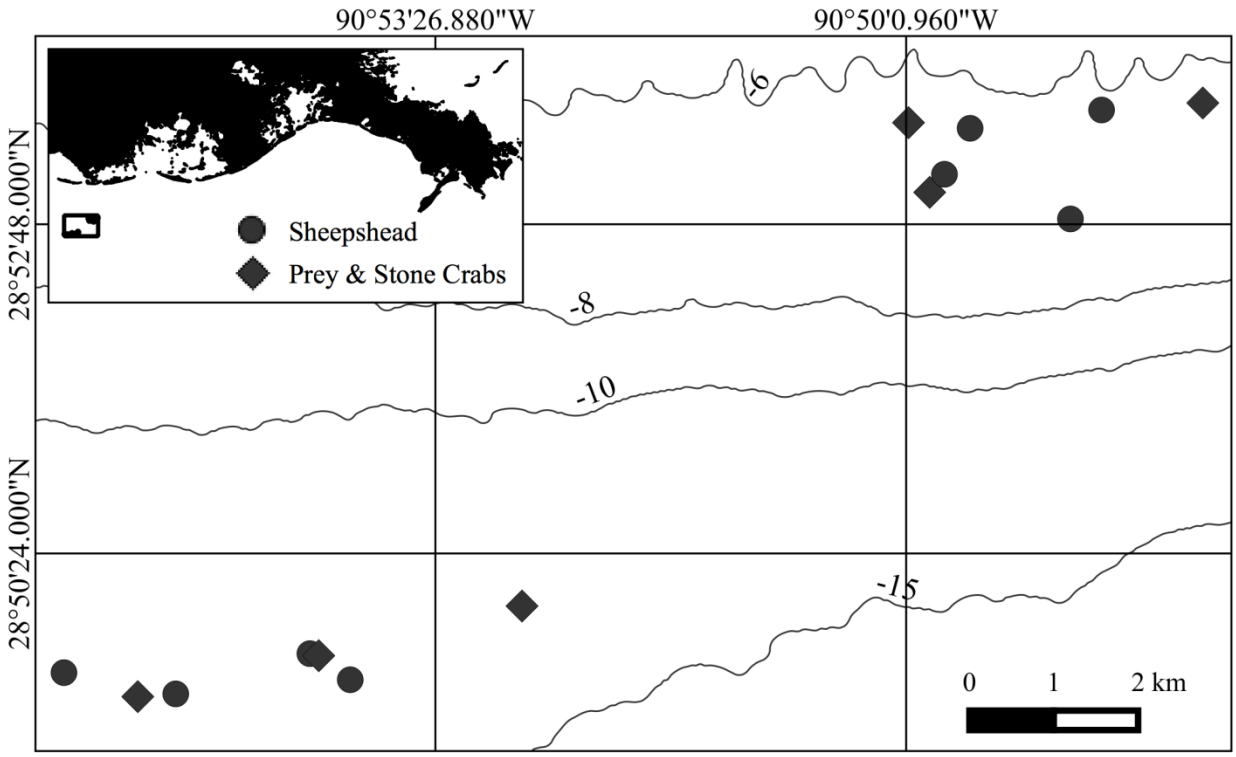

Figure 5.1. Map of the study area. Black circles denote platforms where Sheepshead were sampled and black diamonds denote platforms where prey (platform-associated macro algae, barnacles, sediment) and stone crabs were sampled. The cluster of platforms in the northeastern part of the map were shoal platforms, and the cluster of platforms in the southwestern part of the map were seaward platforms. Contour lines show the depth in meters.

Gut Contents Analysis

Gravimetric gut contents analysis (Carr and Adams 1972) was used to characterize Sheepshead diet. Prey were removed from the entire digestive tract, dyed with Rose Bengal, and washed through a stack of four sieves (4000, 2000, 1000, 500 μm). Prey were then sorted into

the following categories: macro algae, Amphipoda, Balanidae, Bryozoa, Menippidae, Muricidae, Nassariidae, Ostreidae, Panaeidae, Polychaeta, Portunidae, sediment, Squillidae, unknown, Veronidae, and Xanthidae. All prey in the 4000 and 2000 μm sieves were characterized, and 25% from the 1000 and 500 μm sieves were randomly subsampled and used to characterize the prey. Prey were dried for 12 hours at 70ºC and weighed to the nearest 0.001 g. Dry weights were used to calculate percent composition of each prey item.

Table 5.1. Number of sheepshead and stone crabs, whether platform associated macro algae, barnacles, and sediment (sources) were collected (Y = yes, N = no), and number of platforms where Sheepshead and benthos (stone crabs, platform associated algae, barnacles, sediment) were collected at shoal and seaward platforms (Sea) in 2016. Dates denote the date in 2016 when samples in individual rows were collected.

Date	**Sheepshead (Shoal, Sea)**	**Stone Crabs (Shoal, Sea)**	**Sources (Shoal, Sea)**	**Sheepshead Platforms (Shoal, Sea)**	**Benthos Platforms (Shoal, Sea)**
May 31	14, 0	3, 3	Y, Y	2, 0	1, 1
Jun 27	4, 9	3, 3	Y, Y	1, 2	1, 1
Jul 20	0, 0	3, 3	Y, Y	0, 0	1, 1
Aug 19	0, 8	0, 3	N, Y	0, 2	0, 1
Aug 21	0, 0	0, 3	N, Y	0, 0	0, 1
Sep 7	0, 0	6, 0	Y, N	0, 0	2, 0
Sep 11	9, 0	3, 3	Y, Y	2, 0	1, 1

Stable Isotopes Sample Preparation and Analysis

Analyses of $\delta^{13}C$ and $\delta^{15}N$ were performed on Sheepshead liver and muscle, stone crab claw muscle, barnacle muscle, algae, and sediment. Slow and fast turnover tissues (liver and muscle, respectively) were utilized for Sheepshead because they are thought to migrate offshore from inshore waters during the cooler months (Springer and Woodburn 1960; Jennings 1985; Tremain et al. 2004), and thus slower turnover tissue may not reflect offshore diets in the early summer. Three stone crabs and 5–10 barnacles were randomly subsampled from each collection

(12 total collections). Muscle was extracted from stone crab claws, beneath barnacle moveable plates (retractor muscle), and from Sheepshead epaxial muscle. The entire Sheepshead liver was extracted. Stone crab and Sheepshead tissues were analyzed separately, but barnacles were pooled from each collection to obtain sufficient material for analyses. Stone crab muscle, barnacle muscle, and algae were then cleaned of shell fragments and other debris under a dissecting microscope. All samples (Sheepshead liver and muscle, stone crab muscle, barnacle muscle, algae, sediment) were dried in an oven at 60ºC for 24 hours, and were ground into a fine powder using a mortar and pestle. Barnacle muscle, algae, and sediment were acid fumigated under vacuum in glass dishes for 72 hours using concentrated HCl to remove carbonates (Harris et al. 2001), and were then dried for an additional 24 hours. We encapsulated 1.25 mg of Sheepshead liver and muscle, stone crab muscle, and barnacle muscle; 3.0 mg of algae; and 60 mg of sediment in tin capsules. Encapsulated samples were sent to UCD-SIF and analyzed for $\delta^{13}C$ and $\delta^{15}N$ using a PDZ Europa ANCA-GSL (Automated Nitrogen Carbon Analyzer- Gas Solids and Liquids) elemental analyzer (UC-SIF 2017). Stable isotope values were expressed as δ (‰) and calculated with the following:

$$\delta X = \{[(R_{sample} / R_{standard}) - 1] \times 1000\}$$

where X is ^{13}C or ^{15}N, R_{sample} is ^{13}C / ^{12}C or ^{15}N / ^{14}N of the sample, and $R_{standard}$ is ^{13}C / ^{12}C or ^{15}N / ^{14}N of the standard. Vienna PeeDee Belemite and atmospheric N_2 were the standards for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Statistical Analyses

A combination of frequentists and Bayesian statistical methods were used to analyze data. Frequentists methods were used for analyses of Sheepshead and stone crab biometrics, Sheepshead gut contents, and stable isotopes of sources. Bayesian methods were used for

analyses of Sheepshead and stone crab stable isotopes. The reported measure of error was one standard error for frequentist and the 95% credible interval for Bayesian analyses. A significance level of 0.05 was utilized and significance levels for post-hoc comparisons following ANOVAs were corrected using Tukey-Kramer adjustments (Day and Quinn 1989). Individual Sheepshead and stone crabs were treated as the sampling unit for comparisons of their diets and biometrics. The absence of a relationships between Sheepshead and stone crab sizes vs. $\delta^{13}C$ and $\delta^{15}N$ suggested there was no need to correct isotope data for size (e.g. Sweeting et al. 2007a, 2007b). We also found no relationship between C:N ratios of Sheepshead and stone crabs to $\delta^{13}C$, which suggested there was no need to correct for lipids (Post et al. 2007).

Stone crab CW and weight, sheepshead FL and weight, and number of prey types (Richness) and Shannon-Weiner diversity (Diversity) of Sheepshead gut contents were compared across location (shoal vs. seaward) and time (early vs. late) with generalized linear models (GLM; Proc Glimmix, SAS 9.4). Location, time, and location-by-time interaction were main effects for all GLMs, and a size covariate was included for Richness, Diversity, and weights of Sheepshead and stone crabs. Richness was assumed to follow a Poisson distribution with a log-link, Diversity was assumed to follow a gamma distribution with a log-link, and length and weight were assumed to follow normal distributions.

Permutational MANOVA (PERMANOVA; Anderson 2001; PRIMER 7) and distance based redundancy analysis (dbRDA; McArdle and Anderson 2001; PRIMER 7) were used to analyze composition of gut contents. The PERMANOVA and dbRDA were run on a Bray-Curtis similarity matrix based on the log(X+1) percent contribution. The PERMANOVA included location, time, location-by-time interaction and a FL covariate as main effects. Loadings for the dbRDA were then plotted in bivariate space, and a vector overlay was added to

display the associations of individual prey types with dbRDA axes. The PERMANOVA and dbRDA only included prey types that occurred in >15% of all samples, and Menippidae and Xanthidae were pooled into their super-family Xanthoidea to meet this criterion.

Trophic breadth analyses of Sheepshead and stone crabs were performed using the SIBER procedure (Jackson et al. 2011; R 3.4.1). Bayesian SIBER ellipse areas were calculated for each location-by-time combination (Early Shoal, Early Seaward, Late Shoal, Late Seaward). SIBER ellipses were plotted in bivariate $\delta^{13}C$ and $\delta^{15}N$ space and were scaled as 95% credible ellipses, which are interpreted as 95% credible intervals.

Bayesian mixing-models of $\delta^{13}C$ and $\delta^{15}N$ were used to estimate the contribution of sources [(barnacles, filamentous algae, sediment, sea lettuce (*Ulva spp.*)] to Sheepshead liver, Sheepshead muscle, and stone crab muscle using the SIMMR procedure (Parnell et al. 2010; R 3.4.1). Exploratory GLMs were performed on sources to compare isotopic values across location, time, and source type to determine groupings. Barnacles were used as a proxy for water column particulate organic matter (WPOM) because they are filter feeders and their isotopic signatures capture long-term isotopic variability (Nerot et al. 2012; Lorrain et al. 2015). The SIMMR procedure was used to incorporate variability resulting from enrichment of $\delta^{13}C$ and $\delta^{15}N$ at higher trophic levels (Parnell et al. 2010). Trophic enrichment factors were designated as 1.3 ± 1.3 (mean ± SD) for $\delta^{13}C$ and 2.9 ± 1.24 for $\delta^{15}N$ (McCutchan et al. 2003). Mixing-models for early and late summer were run separately because of the substantial differences in $\delta^{15}N$ (see results) and since early summer consumers cannot consume late sources. All early mixing-models only considered early sources. Late mixing-models for Sheepshead muscle and stone crabs considered all sources (early and late) because white muscle is a slow turnover tissue (Tieszen et al. 1983; Hesslein et al. 1993; Logan et al. 2006) that likely reflected

the entire summer. However, we only considered late sources for Sheepshead liver because liver quickly turns over (Tieszen et al. 1983; Hesslein et al. 1993; Logan et al. 2006), and it was unlikely that sources from the early summer made a substantial contribution to liver isotope composition in the late summer.

Differences between $\delta^{13}C$ and $\delta^{15}N$ of Sheepshead muscle and liver were visualized using a vector plot. A vector plot of muscle and liver was created where the muscle was treated as the start value and liver was the end value. Vector plots can be used to visualize the differences between past and present feeding by comparing tissues with fast (liver) and slow (muscle) turnover times, and can also be used to make inferences about migration history (Gelpi et al. 2013). Separate vector plots were created for the early and late summer and were overlaid with triangles connecting the three most extreme values of the 95% credible intervals of sources (mixing space).

5.3. Results

Sheepshead and Stone Crab Biometrics

There were no significant differences for Sheepshead and stone crab sizes and weights across location and time. Mean (± SE) Sheepshead FL (341.5 ± 5.71 mm, range: 265 – 440) and weight (1018.0 ± 41.82 g, range: 425 – 1650) were not significantly related to location (FL: $F_{1,39}$ = 0.7, $P > 0.416$; weight: $F_{1,38}$ = 0.8, $P > 0.367$), time (FL: $F_{1,39}$ = 0.5, $P > 0.485$; weight: $F_{1,38}$ = 1.0, $P > 0.313$), or their interaction (FL: F = 1.3, $P > 0.269$; weight: $F_{1,38}$ = 1.9, $P > 0.173$), but length was significantly associated with weight ($F_{1,38}$ = 433.7, $P < 0.001$). Similarly, mean stone crab CW (46.4 ± 1.96 mm, range: 25 – 70) and weight (40.4 ± 4.93 g, range: 5 – 119) were not significantly related to location (FL: $F_{1,32}$ = 3.7, $P > 0.062$; weight: $F_{1,31}$ = 0.2, $P > 0.663$), time (FL: $F_{1,32}$ = 0.0, $P > 0.872$; weight: $F_{1,31}$ = 2.3, $P > 0.14$), or their interaction (FL: $F_{1,32}$ =

2.0, $P > 0.162$; weight: $F_{1,31} = 0.0$, $P > 0.868$), but CW was significantly associated with weight ($F_{1,31} = 404.0$, $P < 0.001$).

Sheepshead Gut Contents

Organisms from 17 taxonomic groups were identified in Sheepshead guts (Table 5.2). The most abundant organisms were barnacles (Balanidae), which occurred in 96% of all samples and represented 64.1% ± 5.49 of prey by weight found in Sheepshead guts. All guts contained some unidentified content, but mean unidentified content was only 5.8% ± 1.09. All guts contained identifiable prey.

Diversity of Sheepshead gut contents was consistent at shoal platforms and declined at seaward platforms from early to late summer, but Richness did not change across location or time. GLMs indicated there was a significant location-by-time interaction for diet Diversity ($F_{1,39} = 6.8$, $P < 0.013$), which suggested that there was divergence of Sheepshead diet at shoal and seaward platforms. However, there was no significant effect of location ($Z = 3.6$, $P > 0.059$), time ($Z = 0.3$, $P > 0.565$), or their interaction ($Z = 1.0$, $P > 0.323$) on diet Richness (overall mean: 4.2 ± 0.24). Post-hoc comparisons of diet Diversity indicated that LS means were similar at shoal and seaward platforms early in the summer (0.5 ± 0.15 vs. 0.5 ± 0.11), but seaward platforms had significantly lower diet Diversity than shoal platforms during the late summer (0.1 ± 0.03 vs. 0.5 ± 0.14). There was no significant effect of FL on diet Richness ($Z = 0.2$, $P > 0.656$) or Diversity ($F_{1,39} = 0.1$, $P > 0.811$).

The composition of prey in Sheepshead guts changed across location and time. The PERMANOVA indicated that there was a significant location-by-time interaction (Pseudo-$F_{1,39} = 2.9$, $P < 0.034$) on prey composition, but there was no significant effect of size (Pseudo-$F_{1,39} = 2.3$, $P > 0.063$). However, PERMDISP (distance-based test for homogeneity of multivariate

dispersions; Anderson 2006) indicated that the assumption of homogenous variances was violated and that differences were in-part driven by heteroscedasticity (location-by-time: $F_{3,40}$ = 11.4, $P < 0.001$). The dbRDA explained 71.4% of the differences in diet composition (Figure 5.2) and corroborated the findings of the PERMANOVA and PERMDISP. Dispersion of diet composition was generally higher during the early summer than it was in late summer, and dispersion during the late summer at seaward platforms was substantially smaller than other location-by-time combinations. During the early summer Portunidae, Nassariidae, Bryozoa and Balanidae made greater contribution to diet composition at shoal platforms, whereas Squillidae and Xanthoidea made greater contributions at seaward platforms. During the late summer, diet composition in both locations was dominated by Balanidae.

Table 5.2: Mean percent composition, standard error, and percentage of guts where individual prey items occurred for all sampled Sheepshead.

Prey	**Mean Percent Composition**	**SE**	**Percent Occurrence**
Balanidae	64.1	5.49	96
Portunidae	9.9	3.74	27
Squillidae	7.3	3.44	18
Unknown	5.8	1.09	100
Nassariidae	2.6	1.76	32
Menippidae	2.3	1.06	25
Bryozoa	1.5	0.47	61
Sediment	1.4	0.60	39
Algae	0.8	0.26	32
Xanthidae	0.5	0.34	14
Panaeidae	0.4	–	7
Unidentified Crab	0.4	–	5
Amphipoda	0.3	0.16	25
Ostreidae	0.2	0.11	16
Muricidae	0.1	0.06	15
Veneroidae	0.1	0.05	11
Polychaeta	<0.1	–	5

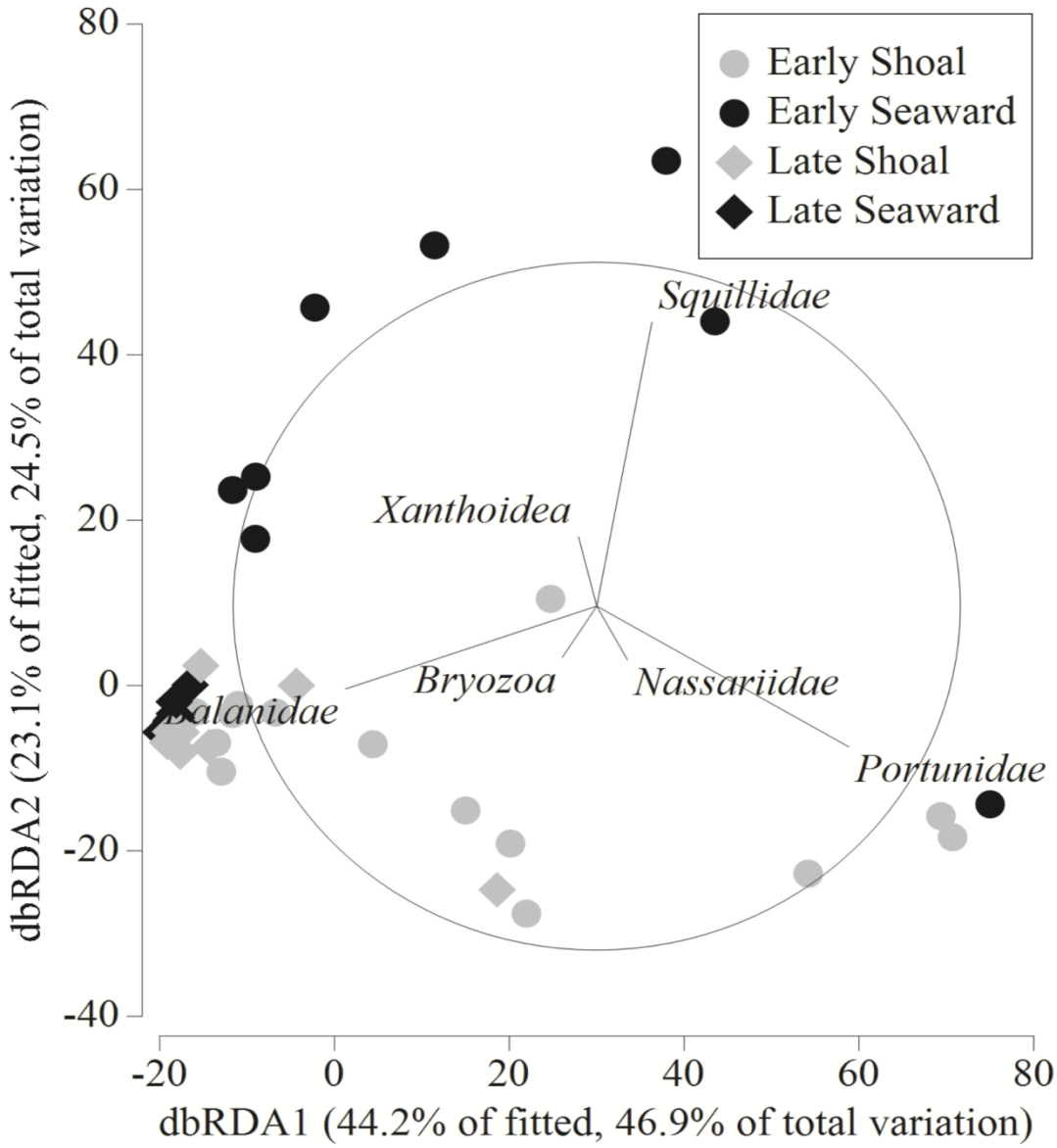

Figure 5.2. Distance based redundancy analysis (dbRDA) showing the similarity of Sheepshead prey at shoal and seaward platforms during the early and late summer. Prey items were plotted when Pearson correlations between dbRDA axes 1 and 2 were greater than 0.15, and the radii are scaled to the plotted circle of radius 1.0 (perfect correlation).

Dispersion of $\delta^{13}C$ and $\delta^{15}N$ Values for Sheepshead and Stone Crab

SIBER ellipses of consumers' $\delta^{13}C$ and $\delta^{15}N$ values showed overlap across time and location, but there was broader dispersion of early consumers at shoal platforms than all other location-by-time groupings. SIBER ellipses of Sheepshead muscle and stone crab showed broad

overlap of $\delta^{13}C$ and $\delta^{15}N$ values, but Sheepshead liver showed substantial enrichment in $\delta^{15}N$ in the late summer relative to the early summer (Figure 5.3). Stone crab had the smallest SIBER ellipse areas, Sheepshead muscle had the largest, and Sheepshead liver ellipse areas were intermediate (Figure 5.4). While overlap of 95% credible ellipses indicated this trend was mostly insignificant, early consumers at shoal platforms tended to have greater ellipse areas than all other location-by-time combinations (early seaward, late shoal, late seaward). While no Sheepshead sex-specific isotopic differences were observed, $\delta^{15}N$ for stone crab females was more enriched than males. This difference explains the high degree of $\delta^{15}N$ variance observed for stone crabs, but we lacked sufficient sample sizes to analyze the sexes separately.

Patterns of Source $\delta^{13}C$ and $\delta^{15}N$ Values and Groupings for Mixing-Models

Mixing-model sources were grouped as filamentous algae (red algae, brown algae, green algae), sea lettuce, barnacles, and sediment, pooled across both locations, and means were calculated separately for early and late summer. Since $\delta^{13}C$ of all filamentous algae was similar (Table 5.3), they were pooled as a single source, but it should be noted that filamentous algae consisted of unidentified red algae in the early summer and green and brown algae in the late summer. GLMs indicated that there was no significant effect of location for $\delta^{13}C$ ($F_{1,4} = 0.2$, $P > 0.652$) and $\delta^{15}N$ ($F_{1,4} = 2.5$, $P > 0.191$), so sources were pooled across location. $\delta^{13}C$ values of individual sources were comparable during the early and late summer ($F_{1,5} = 3.2$, $P > 0.133$), but a significant effect of time for the $\delta^{15}N$ ($F_{1,5} = 7.0$, $P < 0.047$) suggested there was $\delta^{15}N$ enrichment in the late summer. Due to broad isotopic overlap of barnacles and filamentous algae, they were combined using the "combine_sources" function in SIMMR.

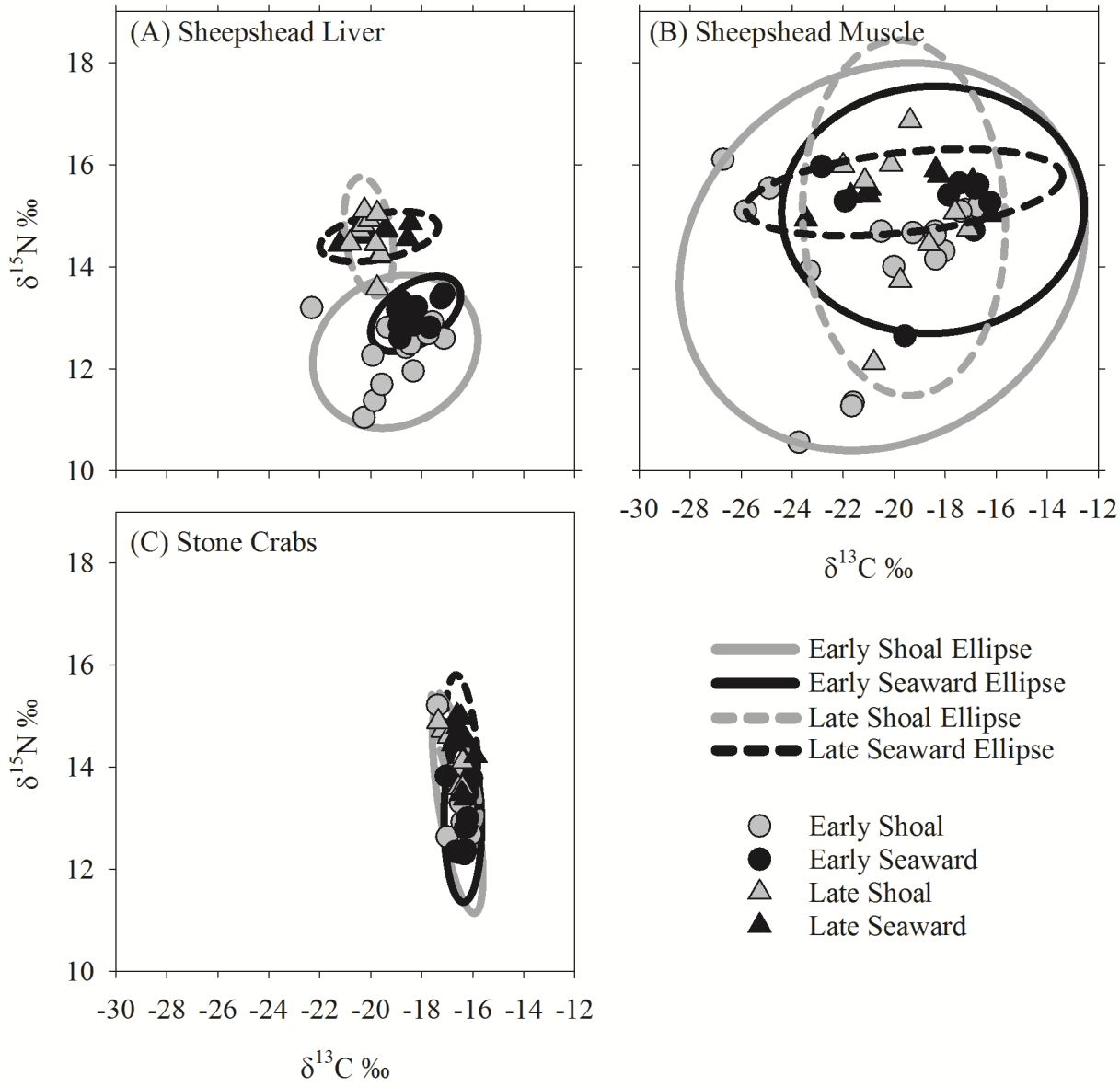

Figure 5.3. Sheepshead liver (A), Sheepshead muscle (B), and stone crabs (C) in bivariate $\delta^{13}C$ and $\delta^{15}N$ with overlaid SIBER ellipses. SIBER ellipses are denoted by solid and dashed lines and represent a 95% confidence ellipse, which are interpreted as 95% confidence intervals (i.e. overlapping ellipses are not significantly different).

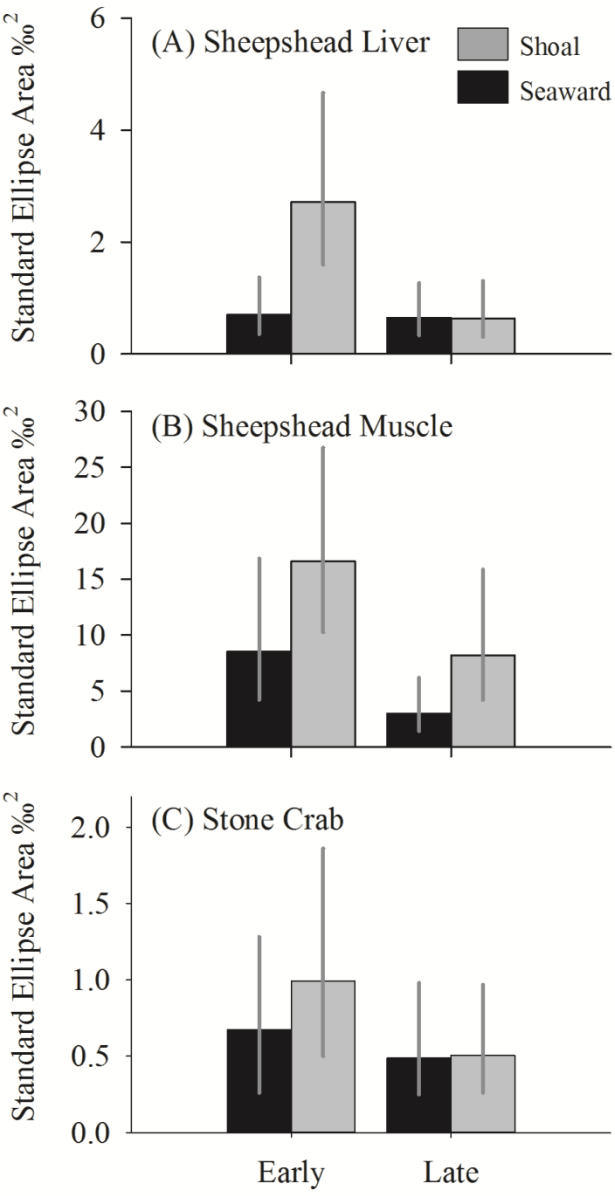

Figure 5.4: Estimates of the standard ellipse areas for Sheepshead liver (A), Sheepshead muscle (B), and stone crabs (C). Black bars denote Sheepshead at seaward platforms and grey bars denote shoal platforms. Error bars represent the 95% credible interval.

Mixing Models

Mixing-models for Sheepshead liver and stone crab showed that platform-associated fauna were the primary source of prey, but no mixing model was run for Sheepshead muscle because isotope values were well outside the mixing space of sources (Figure 5.5C – D).

Sheepshead liver (Figure 5.5A – B) and stone crab muscle isotope values (Figure 5.6A – B) were well constrained within the mixing space of their respective sources. Source contributions to Sheepshead liver were similar across location and time (Figure 5.7A – B), with barnacles/ filamentous algae making the largest contribution (means of 79.2 – 83.0%), sea lettuce making the lowest contribution (means of 5.4 – 6.5%), and sediment making an intermediate contribution (means of 9.8 – 16.6%). Source contributions to stone crabs were similar across location and time (Figure 5.7C – D), with barnacles/ filamentous algae making the largest contribution (means of 67.7 – 76.5%), sediment making the lowest contribution (means of 2.8 – 4.2%), and sea lettuce making an intermediate contribution (means of 19.8 – 27.9%). For all mixing-models, the 95% credible intervals of barnacles/ filamentous algae did not overlap with sediment and sea lettuce, but there was broad overlap between sediment and sea lettuce. There were no significant differences between the early and late summer.

Table 5.3: $\delta^{13}C$, SE (standard error) of $\delta^{13}C$, $\delta^{15}N$, SE of $\delta^{15}N$, and sample sizes (n) of filamentous algae (red algae, green algae, brown algae), sea lettuce, barnacles, and sediment collected in the early (May 31 – Jun 20) and late (Aug 19 – Sep 11) summer of 2016. Brown and green algae were not collected during the early summer, and sea lettuce and red algae were not collected during the late summer.

Source	**$\delta^{13}C$**	**SE**	**$\delta^{15}N$**	**SE**	**n**
		Early			
Red Algae	–19.6	1.83	8.8	0.03	3
Sea Lettuce	–15.4	0.89	8.4	0.04	3
Barnacles	–18.5	0.15	10.9	0.42	6
Sediment	–23.8	0.68	5.2	2.01	5
		Late			
Brown Algae	–20.5	0.15	10.6	0.01	4
Green Algae	–20.0	0.90	10.2	0.42	2
Barnacles	–19.1	0.14	12.9	0.17	6
Sediment	–24.7	1.10	4.8	1.75	6

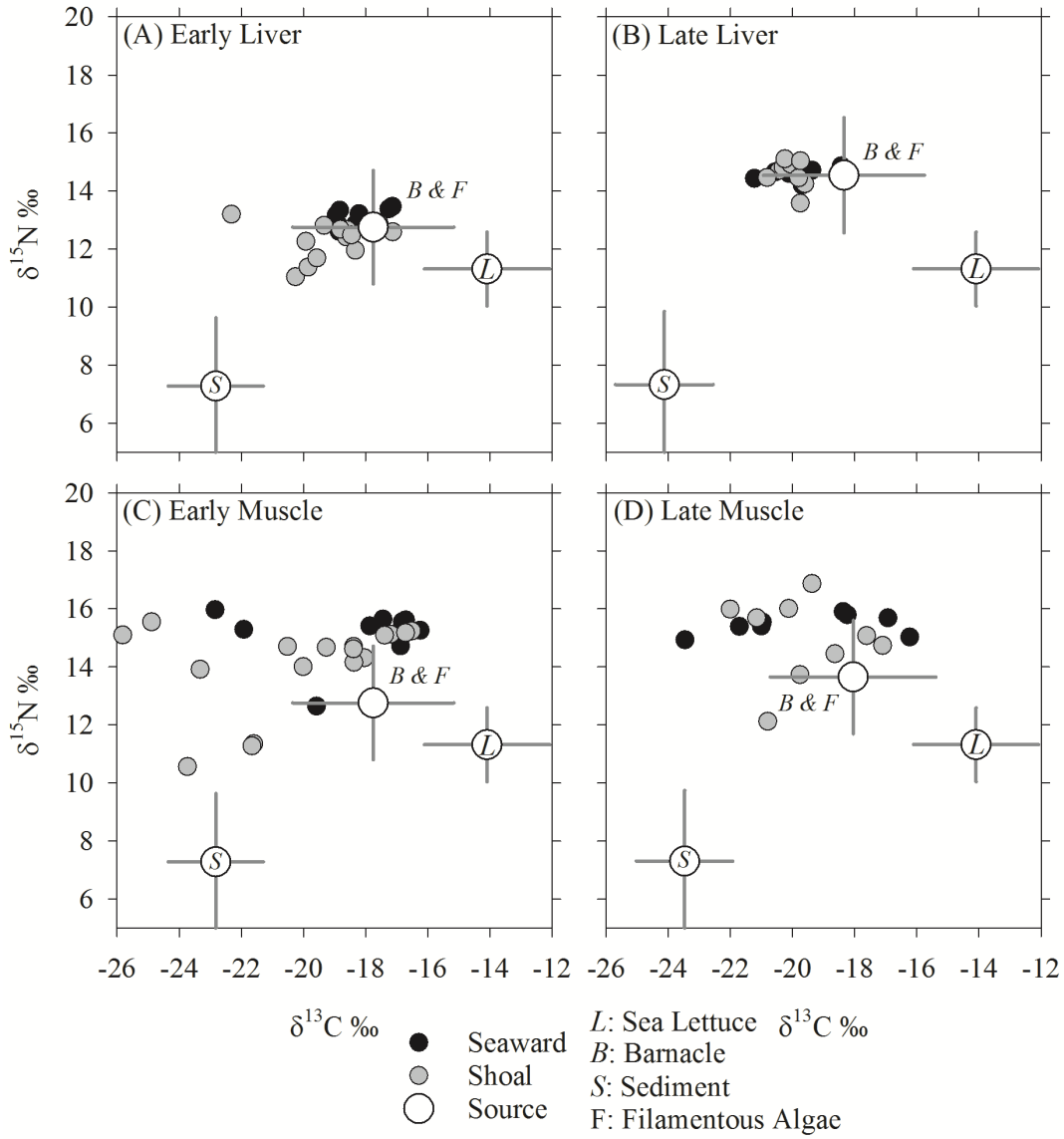

Figure 5.5. Sheepshead liver during the early (A) and late summer (B), and Sheepshead muscle in the early (C) and late summer (D) plotted in bivariate $\delta^{13}C$ and $\delta^{15}N$ along with values of sources (sea lettuce, barnacles, sediment, filamentous algae). Values of sources shown here are corrected for trophic enrichment.

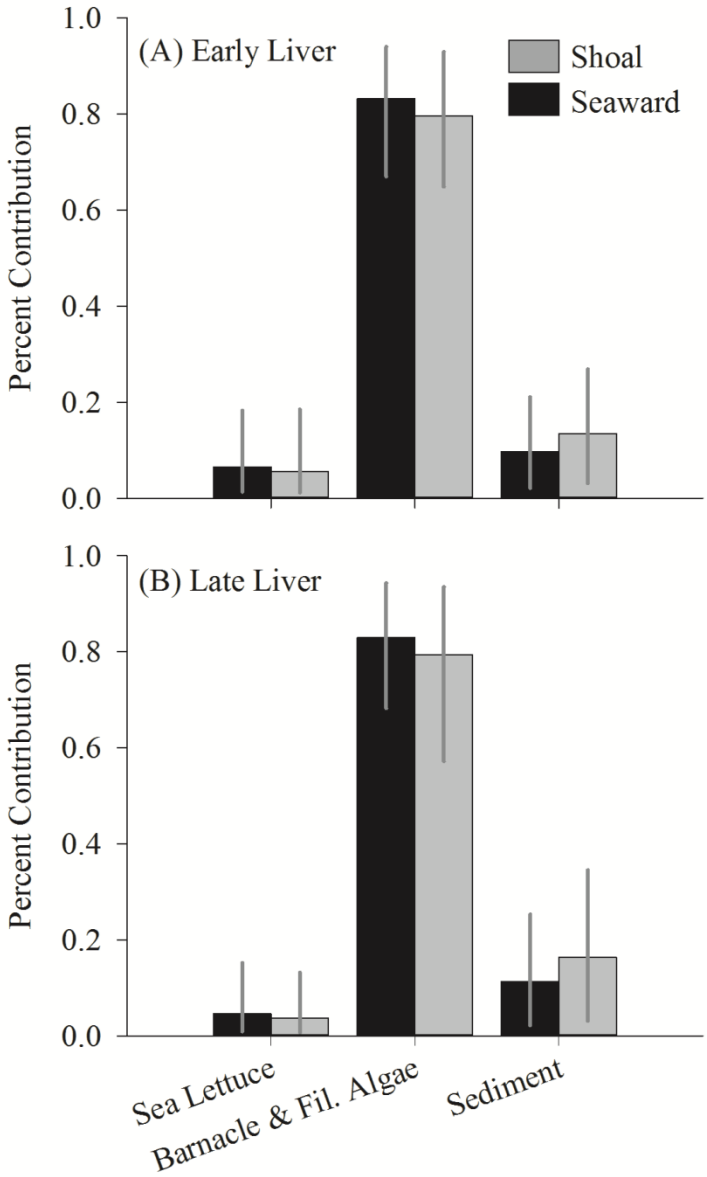

Figure 5.6. Mixing-models for early (C) and late Sheepshead liver (D) showing the percent contribution of sources to Sheepshead diet. Black bars denote Sheepshead at seaward platforms and grey bars denote shoal platforms. Error bars represent the 95% credible intervals.

Vector Plots

The vector plots of Sheepshead muscle and liver indicated large discrepancies between the two types of tissue in the early summer and smaller discrepancies in the late summer (Figure

5.8). Mean (± SE) distance between $\delta^{13}C$ and $\delta^{15}N$ of muscle and liver decreased from 2.81 ± 0.26 ‰ in the early summer to 2.0 ± 0.21 ‰ in the late summer. The largest differences in the early summer (Figure 5.8A) resulted from muscle that was more depleted in $\delta^{13}C$ and enriched in $\delta^{15}N$ than the corresponding liver. There were also differences between muscle and liver during the late summer but differences were variable and there was no clear pattern (Figure 5.8B). Liver $\delta^{13}C$ and $\delta^{15}N$ tended to fall within the mixing space, whereas muscle values were more variable and were often outside of the mixing space.

5.4. Discussion

Early and Late Summer Feeding Ecology

These findings indicated that hypoxia may have briefly affected the diet of Sheepshead associated with platforms, but the effects were not detectable using stable isotopes and were not necessarily negative. Hypoxia is known to decimate the benthos in nearshore Louisiana (Gaston 1985; Baustian and Rabalais 2009), and we expected that this reduction of macrobenthic biomass would result in a transition from bottom to platform-dwelling prey. However, we found there was no detectable effect of hypoxia on stable isotope composition, and there was an episodic increase in consumption of bottom-dwelling prey soon after the formation of hypoxia.

Stable isotope mixing-models of Sheepshead livers and stone crabs showed there were no differences across location (shoal vs. seaward) or time (early vs. late summer), and thus, no detectable effect of the presence of hypoxia on isotopic composition. Our finding is consistent with a previous study that found no effect of hypoxia on $\delta^{13}C$ and $\delta^{15}N$ values of Atlantic Croaker *Micropogonias undulatus* (Mohan and Walther 2016). However, a key difference is that while Atlantic Croaker maintained a benthic isotope signal (Mohan and Walther 2016), Sheepshead livers and stone crabs maintained a high dependence on barnacles (proxy for

WPOM)/ filamentous algae throughout the summer. It is also possible that changes were not detected for stone crabs because claw muscle slowly turns over (Gelpi et al. 2013); although it is unlikely that stone crabs would have switched from platform to bottom-dwelling prey in the late summer since stone crabs are not typically observed on the bottom during the late summer in this area (Reeves et al. 2017b).

Sheepshead gut contents analyses suggested that fishes at seaward platforms exploited large amounts of benthic prey soon after the formation of hypoxia, and that diet Diversity was stable at shoal platforms and declined at seaward platforms. Approximately 78% of Sheepshead at seaward platforms contained mantis shrimp (Squillidae), which made up 35.2 ± 13.56% of their stomach contents. Sheepshead at seaward platforms had benthic diets primarily consisting of mantis shrimp in the early summer and barnacles (Balanidae) in the late summer. Sheepshead have been observed to feed on mantis shrimp (Overstreet and Heard 1982), but they are not reported as common prey (Overstreet and Heard 1982; Sedberry 1987). High consumption of mantis shrimp corresponded to the development of hypoxia at seaward platforms (mid - late June; Reeves et al. 2017a). Fishes are known to exploit benthic organisms that succumb to hypoxia (Pihl et al. 1992), but this was likely an episodic event since the change in gut contents was not corroborated by stable isotope analyses. A strong decline in the diet Diversity of Sheepshead at seaward platforms could indicate that diets become restricted at seaward platforms, but consistent SIBER ellipses during the early and late summer at seaward platforms suggest similar relative contributions of basal resources. Decreases to Diversity were partly driven by decreased predation on stone crabs. Stone crabs suffer hypoxia-related mortality on the bottom and on platform substrate below the oxycline (Reeves et al. 2017b), so higher Sheepshead consumption of stone crab in the early summer may also suggest an effect of

hypoxia. However, since stone crabs were observed to mostly rely on barnacles/ filamentous algae as prey, this shift would not have been apparent from stable isotopes alone.

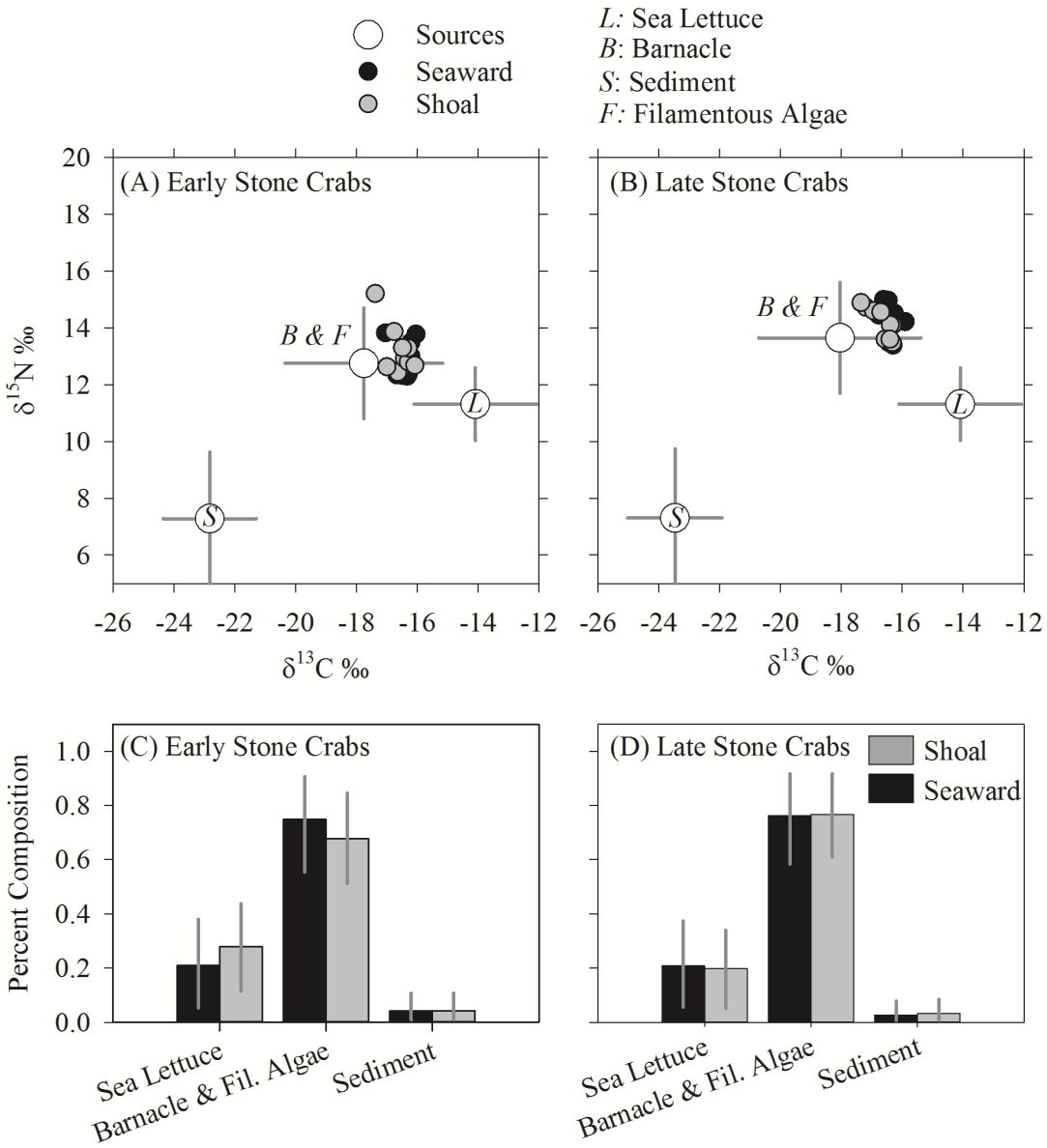

Figure 5.7. Stone crabs during the early (A) and late summer (B) plotted in bivariate $\delta^{13}C$ and $\delta^{15}N$ along with values of sources (sea lettuce, barnacles, sediment, filamentous algae), and mixing-models for early (C) and late stone crabs (D) showing the percent contribution of sources to stone crab diet. Values of sources shown here are corrected for trophic enrichment. Black bars denote Sheepshead at seaward platforms and grey bars denote shoal platforms. Error bars represent the 95% credible intervals.

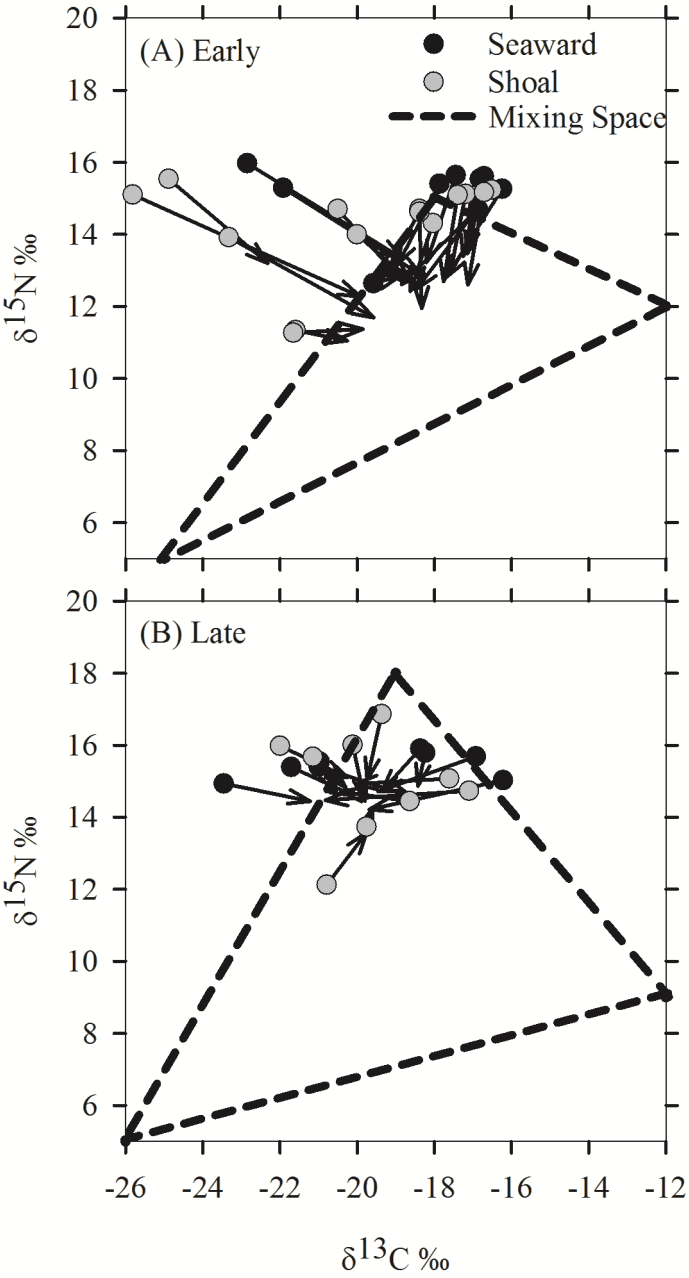

Figure 5.8. Vector plots showing $\delta^{15}N$ and $\delta^{13}C$ of Sheepshead muscle and liver in the early (A) and late summer (B). The $\delta^{15}N$ and $\delta^{13}C$ of muscle is denoted by the black and grey circles and the $\delta^{15}N$ and $\delta^{13}C$ of the corresponding liver is denoted by the point of the arrow. The dashed line denotes the area of sources (sea lettuce, barnacles & filamentous algae, sediment) from each time period.

Contribution of Platform-Dwelling Prey to Sheepshead and Stone Crab Diets

Stable isotopes and gut contents analyses suggested that Sheepshead and stone crabs fed upon a variety of prey associated with platforms. Since Sheepshead liver and stone crab isotope values implied a strong connection to barnacles/ filamentous algae and to a lesser degree, sea lettuce, we consider platform associated algae and filter feeders as important components of their diets. It is possible that some bottom-dwelling filter feeders contributed to the strong barnacles/ filamentous algae signal. However, bottom-dwelling filter feeders should have different $\delta^{13}C$ signals than barnacles/ filamentous algae, because $\delta^{13}C$ of bottom-dwelling filter feeders is known to differ from WPOM (Grippo et al. 2011). Since Sheepshead and stone crab isotope values were tightly clustered around barnacles/ filamentous algae and bottom-dwelling filter feeders were uncommon in Sheepshead guts, it is likely that platform-dwelling prey were the dominant resource. Moreover, barnacles represented ~ 64% of all Sheepshead gut contents and past studies indicated that barnacles are common prey of Sheepshead (Hoskin 1980; Gallaway et al. 1981; Overstreet and Heard 1982; Hoskin and Reed 1984; Sedberry 1987; Hernandez and Motta 1997; Lenihan et al. 2001) and stone crabs (Powell and Gunter 1968; Gallaway et al. 1981). Recent research has begun to evaluate the magnitude and importance of secondary production at artificial reefs (Daigle et al. 2013; Claisse et al. 2014; Cresson et al. 2014a, 2014b; Champion et al. 2015; Reeves et al. 2018). While secondary production on artificial reefs is important to some reef associated organisms, it does not benefit all fishes (Cowan and Rose 2016).

Potential for Contribution from Benthic Microalgae

Benthic microalgae (BMA) were not extracted in these analyses and while it may have contributed to Sheepshead and stone crab diets, its contribution could have been masked by other

sources included in the analyses. BMA are abundant on the shoal (Baustian et al. 2011) and their biomass is thought to exceed the overlying phytoplankton biomass (Grippo et al. 2010). BMA may contribute 53.4 – 83% and 14.5 – 47.7% to the carbon in macroinfauna on and off the shoal, respectively (Grippo et al. 2011). The $\delta^{15}N$ and $\delta^{13}C$ of BMA is indistinguishable from sediment isotopes off the shoal throughout the year and on the shoal during spring and summer (Gelpi et al. 2013). Due to the broad overlap of sediment and BMA, we interpreted contributions of sediment as a general benthic source that represents BMA, settled phytoplankton, and other organic materials in the surface sediment. Gelpi et al. (2013) reported substantial differences between BMA and sediment in the autumn when BMA was more enriched in $\delta^{13}C$ than sediment. The $\delta^{13}C$ values we observed for sea lettuce broadly overlapped with those reported for autumn BMA by Gelpi et al. (2013). The lack of a notable contribution of sea lettuce in the late summer suggests that either sediment and BMA had not diverged, or that BMA was not making a meaningful contribution to Sheepshead livers. Sea lettuce was observed to make a substantial contribution to stone crabs in the late summer (19.8 – 27.9%), and it is possible that enriched BMA was contributing to this signal; however, it is unlikely that stone crab claw muscle had sufficiently turned over to reflect this signal.

Evidence of Sheepshead Migration

Discrepancies between the $\delta^{13}C$ and $\delta^{15}N$ in Sheepshead liver and muscle in the early summer and convergence in the late summer suggests that some Sheepshead migrated from outside of the study area before the onset of sampling. Mean distance between the $\delta^{15}N$ and $\delta^{13}C$ of liver and muscle modestly converged from the early to late summer. Convergence seemed to be partly driven by increased $\delta^{15}N$, which may have resulted from higher temperatures during the late summer (e.g. Goering et al. 1990), differences in Mississippi River discharge, and/or higher

nitrogen cycling in the benthos associated with hypoxia (e.g. Fry 2011). However, the largest discrepancies between liver and muscles for Sheepshead in the early summer were fish that had muscle depleted in $\delta^{13}C$ and enriched in $\delta^{15}N$ relative to liver, which is suggestive of landward-seaward movement. Organisms in Louisiana's inshore waters tend to be depleted in $\delta^{13}C$ and enriched in $\delta^{15}N$ (Fry 2002) relative to those in offshore waters (Fry 2011). A similar pattern of $\delta^{15}N$ and $\delta^{13}C$ discrepancies and eventual convergence of fast and slow turnover tissues was previously observed for blue crabs on the shoal following their seaward migration from coastal marshes (Gelpi et al. 2013). Offshore movement of Sheepshead is thought to correspond with seasonal movement in the early autumn for overwintering (Jennings 1985) or spawning (Springer and Woodburn 1960; Tremain et al. 2004), which occurs from February to April (Render and Wilson 1992). While it is possible that Sheepshead migrated from inshore waters in the preceding winter and spring, it is likely that some were offshore residents because we previously observed Sheepshead at nearby platforms throughout the year (D. Reeves, Unpublished Data).

Conclusions

This study underscores the importance of platform-dwelling primary and secondary producers as prey. This is a timely finding because Sheepshead and stone crabs are common on nearshore platforms where barnacle production is substantially higher than it is further offshore (Reeves et al. 2018), yet nearshore platforms are rapidly being removed as oil and gas exploration shifts further offshore (43% reduction since 2006; BOEM 2015). These findings suggest that barnacles and other secondary producers on nearshore platforms may be funneling pelagic production into Sheepshead and stone crab biomass in a region where excessive phytoplankton production is known to fuel hypoxia (Turner and Rabalais 1991, 1994; Rabalais et al. 1996). This process may facilitate the transfer of some of the excessive primary production to

a select group of commercially valuable species, which represents a unique ecosystem service provided by the fouling communities on platforms in the Gulf of Mexico.

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CHAPTER 6: CONCLUSIONS

6.1. The influence of river discharge on fishes and invertebrates associated with small oil and gas platforms in nearshore Louisiana

The Mississippi and Atchafalaya rivers in Louisiana's coastal waters strongly influenced fishes and invertebrates associated with small oil and gas platforms. The influence of river discharge in Louisiana's coastal waters negatively and positively affected reef-associated organisms. High primary productivity associated with river discharge increased secondary production at nearshore platforms, relative to similar changes further offshore. However, coastal eutrophication driven by river discharge also caused the formation of hypoxia which triggered the redistribution of reef-associated organisms.

Nutrient laden river discharge directly and indirectly influenced total platform associated secondary productivity (Figure 6.1). Fouling accumulation, barnacle settlement, and barnacle growth were markedly higher in nearshore waters where there was prolific primary and secondary production. It is well established that barnacle growth and settlement is greater in areas with higher phytoplankton (Bertness et al. 1991; Menge et al. 2003; Leslie et al. 2005) and zooplankton production (Sanford and Menge 2001). Primary and secondary production are generally greater closer to shore and in the surface waters off Louisiana's coast (Chen et al. 2000). The plankton and secondary production is especially high off Louisiana's coast, driven by nutrient laden discharge from the Mississippi and Atchafalaya rivers (Dortch and Whitledge 1992; Justić et al. 1993; Dagg and Breed 2003). Thus, the high plankton productivity off coastal Louisiana undoubtedly stimulates the observed differences in barnacle settlement and growth. Barnacles were shown to be important prey for Sheepshead *Archosargus probatocephalus* (Figure 6.2) and stone crabs *Menippe* spp., which suggested that high productivity associated with river discharge has the capacity to support the growth of platform-associated organisms. It

may also enhance the total secondary production of these species by shunting primary production into platform associated food webs.

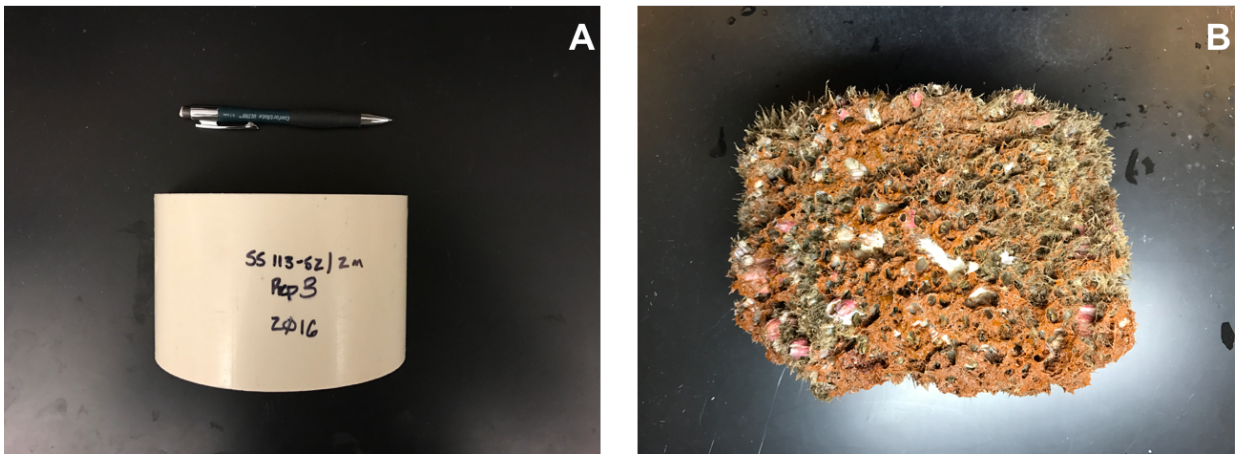

Figure 6.1: Settlement plate before (A) and after (B) a 92-day deployment in 2016. The plate was deployed at 2.0 m and was 23.1 km from shore.

Hypoxia strongly affected the vertical depth distributions of fishes and invertebrates, but there was no clear evidence of negative trophic consequences for Sheepshead and stone crabs. Hypoxia resulted in the vertical redistribution of fishes at platforms with hypoxic bottom waters and excluded barnacles and blennies from waters near the bottom. This reduction to the amount of available space is often referred to as hypoxia-based habitat compression and is consistent with previously reported patterns of fish redistribution, which showed that high densities of fishes occurred in the waters just above hypoxia around platforms (Stanley and Wilson 2004). Hypoxia-based habitat compression is known to be associated with the vertical redistribution of organisms in the nGOM (Stanley and Wilson 2004; Hazen et al. 2009; Roman et al. 2012). Avoidance of bottom waters may ultimately limit the access of reef-associated organisms to prey living on the seafloor (e.g. Lenihan et al. 2001), but Sheepshead and stone crab diets did not shift away from bottom-dwelling prey in response to hypoxia. Rather, gut contents analysis indicated

that Sheepshead fed more intensely on benthic prey soon after the formation of hypoxia (e.g. Pihl et al. 1992), and Sheepshead were sometimes observed to briefly enter hypoxic waters where they may have been exploiting dead or dying benthos. Nevertheless, Sheepshead diets eventually reverted to being dominated by barnacles, suggesting that exploitation of vulnerable benthic prey is likely an episodic event.

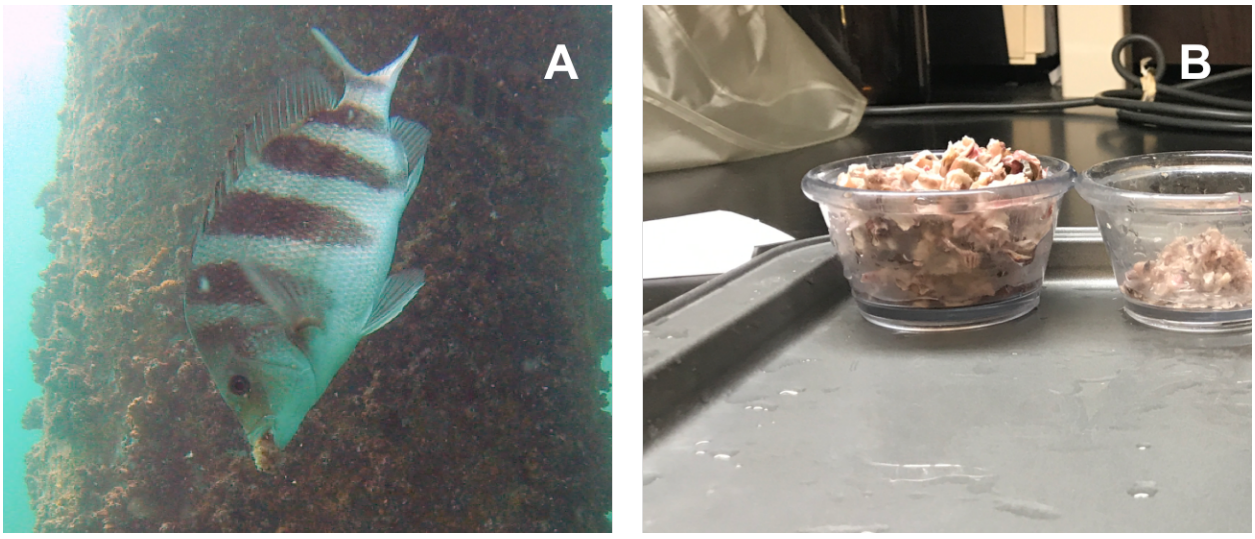

Figure 6.2: Sheepshead with a cluster of barnacles in its mouth (A) and barnacles removed from a Sheepshead gut (B).

6.2. The ecological value of oil and gas platforms

Platforms provide refuge for reef-associated organisms living within the nGOM's hypoxic zone. Platforms span the entire water column providing hard substrate that is utilized by reef-associated organisms in oxygenated waters overlaying hypoxia. This hard substrate is settled by barnacles and other fouling organisms, which provides a source of prey for Sheepshead, Gray Snapper *Lutjanus griseus*, Horse-eye Jack *Caranx latus*, Black Drum *Pogonias cromis*, and Atlantic Spadefish *Chaetodipterus faber*, and stone crabs.

Louisiana's nearshore platforms are highly productive habitats, but platform associated productivity is species-specific. In this study, Sheepshead, Gray Snapper, Horse-eye Jack, Black

Drum, Atlantic Spadefish, and stone crabs were observed to feed on platform-dwelling organisms, and Sheepshead and stone crab were shown to be highly dependent on platform-dwelling prey (barnacles, macro algae). Juvenile Gray Snapper *Lutjanus griseus* (Figure 6.3) were also observed foraging by 41.7% (5/12) of cameras during August and September. Juvenile Gray Snapper are generalist predators that consume amphipods, shrimp, crabs, and fishes (Franks and Vanderkooy 2000). Juvenile Gray Snapper were uncommon in the study area from May to August, but their abundances around small platforms increased ~400% in August and September. If platforms-dwelling organisms provide a source of prey for juvenile Gray Snapper, it could mark an important ecosystem service because they are a commercially and recreationally important species (commercial landings in the GOM: 131.42 metric tons year^{-1} from 2007-2016; NMFS 2017). Nevertheless, many species of fish that live around platforms were not observed to prey on platform-dwelling organisms. These finding support the notion that the degree of attraction or production is unquestionably taxon-specific (Cowan and Rose 2016).

Figure 6.3: Juvenile Gray Snapper observed around an oil and gas platform.

There are other ecological aspects of platforms that are still poorly understood, including their value to pelagic fishes, their effect on fish behavior, and the amount of platform associated primary production. Pelagic fishes were abundant around platforms. One of the most common

pelagic species, Blue Runner *Caranx crysos* (Figure 6.4), is known to establish home ranges around platforms (Brown et al. 2010), and platforms may enhance Blue Runner foraging success by accumulating plankton (Keenan et al. 2003). Fish behavior may also be altered around platforms, especially when hypoxia concentrates fishes in the mid to upper water column (Stanley and Wilson 2004; Chapter 2). Crowding has been hypothesized to increase predator-prey interactions (Breitburg 1994; Eby and Crowder 2002; Eby et al. 2005; Prince and Goodyear 2006, 2007; Hazen et al. 2009; Roman et al. 2012), antagonistic behaviors (Aumann et al. 2006), and stress; which may have consequences for reproduction and growth (Bonga 1997; Mccormick 2006). Future research should also focus on the magnitude of algal production at platforms because it is known to be incorporated into the diets of reef-associated fishes (Daigle et al. 2013; Chapter 5). Developing a better understanding of these aspects is critical for resolving the debate over the ecological value of platforms.

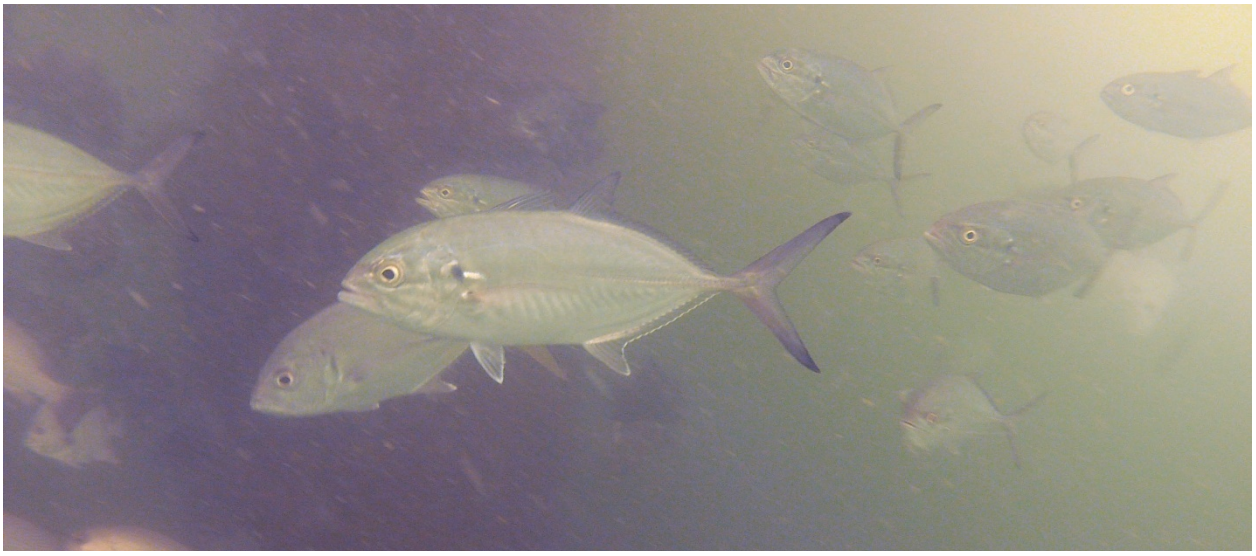

Figure 6.4: Blue Runner around an oil and gas platform.

This dissertation addressed several topics that will help resolve the debate over fisheries productivity at platforms, but significant gaps remain. Those topics include a greater understanding of: (1) the magnitude and spatial variability of secondary production, (2) energy flow and the feeding ecology of reef associated organisms, and (3) the importance of platforms' vertical relief as a refuge from hypoxia and as substrate that enhance secondary production.

6.3. Implications for management

As nearshore platforms are removed, there has been an increasing and continuing loss of recreational and commercial fishing opportunities in Louisiana's nearshore waters as platform numbers have decreased by ~44%. This is important because platforms are popular commercial and recreational fishing sites in Louisiana's coastal waters (Ditton and Auyong 1984; Stanley and Wilson 1989). As the oil and gas industry transitions towards fewer platforms in deep waters off the continental shelf (Pulsipher et al. 2001), opportunities to fish for reef-associated fishes around platforms off Louisiana have been reduced.

The vertical extent of platforms distinguishes them from traditional artificial reefs (Hernandez et al. 2003; Stanley and Wilson 2004), and is a key aspect of their ecological value in the nGOM. Since shallow-water platforms are quickly being removed, it is important to implement artificial reef management plans that focus on reducing deleterious consequences of losing the unique function that platforms provide. Inclusion of standing platforms in Louisiana's Rigs-to-Reefs program is unlikely because of significant maintenance costs and liability associated with standing platforms (Kaiser 2006). In order for artificial reef placements to be successful, they should be where hypoxia is uncommon or include enough relief to provide a hard structure refuge above the vertical extent of hypoxia. The relief required to exceed the vertical extent of hypoxia (3–4 m) could still pose a hazard to navigation, but this issue should be

explored since platforms in areas with intense hypoxia may provide particularly important benefits to fisherman targeting reef associated fishes. Furthermore, Louisiana's sandy shoals should be considered as artificial reef planning areas because their propensity to maintain oxygenated bottom waters would enhance the success of lower-relief artificial reefs.

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APPENDIX A: LITERATURE REVIEW OF NORTHERN GULF OF MEXICO PLATFORM RESEARCH

Appendix A: Citations and descriptions of study themes for all northern Gulf of Mexico papers reviewed.

Citation	Study Theme
(Ajemian et al. 2015b)	Fish Assemblages
(Ajemian et al. 2015a)	Fish Assemblages
(Barker and Cowan 2017)	Fish Assemblages
(Beaver et al. 2003)	Secondary Production
(Boswell et al. 2010)	Hydroacoustics
(Brown et al. 2010)	Blue Runner Movement
(Bull et al. 2008)	Review
(Bull and Kendall 1994)	Fish Assemblages; Invertebrate Assemblages
(Cowan and Rose 2016)	Review
(Daigle et al. 2013)	Food Webs
(Fischer et al. 2004)	Red Snapper Life History
(Gallaway et al. 1981)	Fish Assemblages; Invertebrate Assemblages; Food Webs
(Gallaway et al. 2009)	Review
(Gitschlag et al. 2003)	Red Snapper Life History
(Glenn et al. 2017)	Red Snapper Life History
(Gunter and Geyer 1955)	Invertebrate Assemblages
(Gupta and Smith 2013)	Foraminifera Assemblages
(Hernandez et al. 2003)	Fish Assemblages
(Karnauskas et al. 2016)	Red Snapper Life History
	Blue Runner Feeding Ecology
(Kolian et al. 2017)	Invertebrate Assemblages
(Kulaw et al. 2017)	Red Snapper Life History
(Lewbel et al. 1987)	Invertebrate Assemblages
(Lindquist et al. 2005)	Fish Assemblages
(Nieland and Wilson 2003)	Red Snapper Life History
(Pie et al. 2015)	Invertebrate PAH Concentrations
(Rademacher and Render 2003)	Fish Assemblages
(Rauch 2003)	Fish Assemblages
(Reeves et al. 2017)	Stone Crab Density and Life History
(Render and Wilson 1994)	Red Snapper Life History
(Sammarco et al. 2004)	Invertebrate Assemblages
(Sammarco et al. 2012a)	Invertebrate Assemblages

(Sammarco et al. 2012b)	Coral Genetics
(Sammarco et al. 2014)	Invertebrate Assemblages
(Sammarco et al. 2015)	Invertebrate Assemblages
(Sammarco et al. 2017)	Coral Genetics
(Schwartzkopf and Cowan 2016)	Red Snapper Life History
(Schwartzkopf et al. 2017)	Red Snapper Feeding Ecology
(Simonsen et al. 2015)	Red Snapper Feeding Ecology
(Sluis et al. 2013)	Red Snapper Feeding Ecology
(Sonnier et al. 1976)	Fish Assemblages
(Stanley and Wilson 1990)	Fish Assemblages
(Stanley and Wilson 1991)	Fish Assemblages
(Stanley and Wilson 1997)	Fish Assemblages; Hydroacoustics
(Stanley and Wilson 2000)	Fish Assemblages; Hydroacoustics
(Stanley and Wilson 2003)	Fish Assemblages; Hydroacoustics
(Stanley and Wilson 2004)	Fish Assemblages; Hydroacoustics
(Streich et al. 2017a)	Fish Assemblages
(Streich et al. 2017b)	Red Snapper Life History
(Topolski and Szedlmayer 2004)	Fish Assemblages

Ajemian, M. J., J. J. Wetz, B. Shipley-Lozano, J. Dale Shively, and G. W. Stunz. 2015a. An Analysis of Artificial Reef Fish Community Structure along the Northwestern Gulf of Mexico Shelf: Potential Impacts Of "rigs-to-reefs" Programs. PLoS ONE 10(5):1–23.

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APPENDIX B: AIC SELECTION CRITERIA FOR ALL FEASIBLE MODELS EXAMINING TRENDS OF FOULING ACCUMULATION, BARNACLE SETTLEMENT, AND BIOMETRICS.

Appendix B: Comparisons of Akaike's Information Criteria (AIC) for all feasible models examining trends of fouling accumulation, barnacle settlement, and biometrics. "Y" denotes the dependent variable for each table, "X1" – "X7" denote the dependent variables, "km" denotes distance from shore (km), "Yr" denotes an indicator variable for year (2015 = 1; 2016 = 0), "m" denotes an indicator variable for depth (2m = 1; 7m = 0), and "*" indicates interaction between variables. The model highlighted in yellow was the final model selected for each comparison.

Y = Fouling Accumulation (g m^{-2} d^{-1})

X1	X2	X3	X4	X5	X6	X7	AIC
km	Yr	m	km*Yr	km*m	Yr*m	km*Yr*m	479.70
km	Yr	m	km*Yr	km*m	Yr*m		485.50
km	Yr	m	km*m	Yr*m			488.20
km	Yr	m	km*Yr	Yr*m			493.00
km	Yr	m	Yr*m				495.70
km	Yr	m	km*Yr	km*m			497.60
km	Yr	m	km*m				502.00
km	Yr	m	km*Yr				504.00
Yr	m	Yr*m					505.50
km	Yr	m					508.00
km	m	km*m					512.30
Yr	m						516.50
km	m						517.80
km	Yr	km*Yr					523.70
m							525.60
km	Yr						527.20
km							537.60
Yr							541.10
int.							550.60

Y = *Amphibalanus* spp. Post-Spat (number m^{-2} d^{-1})

X1	X2	X3	X4	X5	X6	X7	AIC
km	Yr	m	km*Yr	km*m	Yr*m	km*Yr*m	553.40
km	Yr	m	km*Yr	km*m	Yr*m		573.10
km	Yr	m	km*m	Yr*m			577.50
km	Yr	m	km*Yr	Yr*m			586.30
km	Yr	m	km*Yr	km*m			588.00
km	Yr	m	Yr*m				591.20
km	Yr	m	km*m				592.50
Yr	m	Yr*m					598.30
km	Yr	m	km*Yr				602.70
km	m	km*m					603.40
km	Yr	m					607.80
Yr	m						614.30
km	Yr	km*Yr					618.50
km	m						619.20
km	Yr						623.90
m							625.80
Yr							633.70
km							635.20
Int.							645.20

Y = ln[*Amphibalanus* spp. Spat (number m^{-2} d^{-1})]

X1	X2	X3	X4	X5	X6	X7	AIC
km	Yr	m	km*Yr	km*m	Yr*m	km*Yr*m	135.50
km	Yr	m	km*Yr	km*m	Yr*m		144.30
km	Yr	m	Yr*m				144.40
km	Yr	m	km*Yr	Yr*m			144.60
km	Yr	m	km*m	Yr*m			144.70
Yr	m	Yr*m					145.00
km	Yr	m	km*Yr	km*m			146.20
km	Yr	m	km*Yr				147.20
km	Yr	m	km*m				147.40
km	Yr	km*Yr					148.50
Yr	m						149.00
Yr							149.70
km	Yr	m					150.80
km	Yr						152.00
km	m	km*m					156.30
m							157.40
Int.							158.20
km	m						160.20
km							161.50

Y = ln[*Megabalanus tintinnabulum* Post Spat (number m^{-2} d^{-1})]

X1	X2	X3	X4	X5	X6	X7	AIC
Yr	m	Yr*m					120.40
Yr	m						121.30
km	Yr	m	Yr*m				127.10
km	Yr	m					128.00
km	Yr	m	km*m	Yr*m			129.20
km	Yr	m	km*m				130.40
km	Yr	m	km*Yr	Yr*m			132.70
km	Yr	m	km*Yr				133.70
km	Yr	m	km*Yr	km*m	Yr*m		134.60
km	Yr	m	km*Yr	km*m			135.60
km	Yr	m	km*Yr	km*m	Yr*m	km*Yr*m	136.60
m							137.30
km	m	km*m					139.40
Yr							140.10
km	Yr						143.00
km	m						143.40
Int.							147.70
km	Yr	km*Yr					148.10
km							151.30

Y = ln[*Megabalanus tintinnabulum* Spat (number m^{-2} d^{-1})]

X1	X2	X3	X4	X5	X6	X7	AIC
Int.							-278.70
m							-272.30
Yr							-272.10
Yr	m						-265.80
km							-265.10
Yr	m	Yr*m					-261.10
km	Yr						-258.60
km	m						-257.90
km	Yr	m					-251.30
km	m	km*m					-250.30
km	Yr	km*Yr					-247.10
km	Yr	m	Yr*m				-246.90
km	Yr	m	km*m				-243.80
km	Yr	m	km*Yr				-239.70
km	Yr	m	km*m	Yr*m			-238.60
km	Yr	m	km*Yr	Yr*m			-234.00
km	Yr	m	km*Yr	km*m			-232.90
km	Yr	m	km*Yr	km*m	Yr*m		-225.90
km	Yr	m	km*Yr	km*m	Yr*m	km*Yr*m	-223.20

Y = *Amphibalanus reticulatus* Height (mm d^{-1})

X1	X2	X3	X4	X5	X6	X7	AIC
km	Yr	m	Yr*m				-6040.01
Yr	m	Yr*m					-6031.32
Yr	m						-6028.81
km	Yr	m	km*m	Yr*m			-6028.73
km	Yr	m	km*Yr	Yr*m			-6025.22
km	Yr	m	km*Yr	km*m	Yr*m		-6014.06
km	Yr	m	km*Yr	km*m			-6007.82
km	Yr	m	km*Yr	km*m	Yr*m	km*Yr*m	-6007.41
km	Yr	m	km*m				-5939.63
km	m	km*m					-5875.32
km	Yr	km*Yr					-5524.99
km	Yr	m					-5345.8
km	m						-3615.67
m							-2331.88
Yr							4966.28
Int.							8001.98
km							D.N.C.
km	Yr						D.N.C.
km	Yr	m	km*Yr				D.N.C.

Y = *Amphibalanus reticulatus* Width (mm d^{-1})

X1	X2	X3	X4	X5	X6	X7	AIC
Int.							-5730.87
Yr							-5729.31
km	Yr						-5722.54
m							-5722.42
Yr	m						-5721.14
km							-5720.76
Yr	m	Yr*m					-5715.97
km	Yr	m					-5715.77
km	m						-5711.89
km	Yr	km*Yr					-5709.39
km	Yr	m	Yr*m				-5708.56
km	Yr	m	km*m				-5706.08
km	m	km*m					-5705.42
km	Yr	m	km*Yr				-5700.49
km	Yr	m	km*m	Yr*m			-5699.80
km	Yr	m	km*Yr	Yr*m			-5695.32
km	Yr	m	km*Yr	km*m			-5693.19
km	Yr	m	km*Yr	km*m	Yr*m		-5686.51
km	Yr	m	km*Yr	km*m	Yr*m	km*Yr*m	-5675.88

Y = ln[Tallness (Height / Width)]

X1	X2	X3	X4	X5	X6	X7	AIC
km	Yr	m	Yr*m				749.40
km	Yr	m	km*m	Yr*m			753.90
km	m						754.30
km	m	km*m					757.30
km	Yr	m					757.70
km	Yr	m	km*Yr	Yr*m			758.30
km							758.40
Yr	m	Yr*m					759.10
km	Yr	m	km*m				760.80
km	Yr						761.40
m							762.50
km	Yr	m	km*Yr	km*m	Yr*m		762.80
Yr	m						764.30
km	Yr	m	km*Yr				764.60
km	Yr	m	km*Yr	km*m	Yr*m	km*Yr*m	767.20
km	Yr	m	km*Yr	km*m			767.80
Int.							770.20
Yr							771.60
km	Yr	km*Yr					15973.90

Y= ln[*Amphibalanus reticulatus* Total Wet Weight (mg d^{-1})]

X1	X2	X3	X4	X5	X6	X7	AIC
km	Yr	m	km*m	Yr*m			3531.94
km	Yr	m	km*m				3533.71
km	Yr	m	Yr*m				3533.85
km	Yr	m					3534.09
km	Yr						3536.66
km	Yr	m	km*Yr	km*m	Yr*m		3537.80
km	Yr	m	km*Yr	Yr*m			3539.62
km	Yr	m	km*Yr	km*m			3539.80
km	Yr	m	km*Yr				3540.39
km	m	km*m					3540.54
Yr	m	Yr*m					3540.54
Yr	m						3540.64
km	Yr	m	km*Yr	km*m	Yr*m	km*Yr*m	3541.04
km	m						3542.35
km	Yr	km*Yr					3543.05
km							3545.92
Yr							3546.13
m							20122.55
Int.							9037000000000.00

Y = ln[*Amphibalanus reticulatus* Tissue Wet Weight (mg d^{-1})]

X1	X2	X3	X4	X5	X6	X7	AIC
km	Yr	m	Yr*m				3063.51
km	Yr	m	km*m	Yr*m			3068.28
km	Yr	m	km*Yr	Yr*m			3071.24
km	Yr	m	km*Yr	km*m	Yr*m		3075.96
km	Yr						3076.30
km	Yr	m					3077.15
Yr	m	Yr*m					3078.65
km	Yr	m	km*Yr	km*m	Yr*m	km*Yr*m	3079.66
km	Yr	m	km*m				3080.59
km	Yr	km*Yr					3081.80
Yr	m						3082.46
km	Yr	m	km*Yr				3082.50
km	Yr	m	km*Yr	km*m			3086.09
Yr							3086.53
m							3093.10
Int.							3093.25
km	m	km*m					3098.34
km	m						11201.13
km							14933.87

APPENDIX C: AIC SELECTION CRITERIA FOR PERCENT TISSUE

Appendix C: Backwards selection procedure using Akaike's Information Criteria (AIC) for percent tissue [ln(Tissue Wet Weight/ Total Wet Weight)]. "X1" – "X15" denote the dependent variables, "km" denotes distance from shore (km), "Yr" denotes an indicator variable for year (2015 = 1; 2016 = 0), "m" denotes an indicator variable for depth (2m = 1; 7m = 0), Ht. denotes barnacle height (mm), and "*" denotes interaction between variables. The number of variables, AIC, and Δ AIC (difference between given model and the full model) are provided for each model. "Step" denotes whether the given model was selected among models with the same number of variables. The model highlighted in yellow was the final model.

Number of Variables	X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11	X12	X13	X14	X15	AIC	Δ AIC	Step
15	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m	Yr*Ht	m*Ht	km*Yr*m	km*Yr*Ht	km*m*Ht	Yr*m*Ht	km*Yr*m*Ht	660.7	0.0	Yes
14	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m	Yr*Ht	m*Ht	km*Yr*m	km*Yr*Ht	km*m*Ht	Yr*m*Ht		656.8	-4.0	Yes
13	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m	Yr*Ht	m*Ht	km*Yr*m	km*Yr*Ht	km*m*Ht			657.0	-3.7	No
13	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m	Yr*Ht	m*Ht	km*Yr*m	km*Yr*Ht	Yr*m*Ht			645.7	-15.0	Yes
13	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m	Yr*Ht	m*Ht	km*Yr*m	km*m*Ht	Yr*m*Ht			650.2	-10.6	No
13	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m	Yr*Ht	m*Ht	km*Yr*Ht	km*m*Ht	Yr*m*Ht			652.8	-7.9	No
12	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m	Yr*Ht	m*Ht	km*Yr*m	km*Yr*Ht				646.1	-14.6	No
12	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m	Yr*Ht	m*Ht	km*Yr*m	Yr*m*Ht				639.6	-21.1	Yes
12	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m	Yr*Ht	m*Ht	km*Yr*Ht	Yr*m*Ht				641.8	-18.9	No
11	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m	Yr*Ht	m*Ht	km*Yr*m					638.2	-22.5	No
11	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m	Yr*Ht	m*Ht	Yr*m*Ht					635.2	-25.5	Yes
10	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m	Yr*Ht	m*Ht						634.4	-26.3	Yes
9	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m	Yr*Ht							628.9	-31.8	No
9	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m	m*Ht							628.6	-32.1	Yes
9	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*Ht	m*Ht							631.6	-29.1	No
9	km	Yr	m	Ht	km*Yr	km*m	Yr*m	Yr*Ht	m*Ht							645.7	-15.0	No
9	km	Yr	m	Ht	km*Yr	km*Ht	Yr*m	Yr*Ht	m*Ht							628.7	-32.0	No
9	km	Yr	m	Ht	km*m	km*Ht	Yr*m	Yr*Ht	m*Ht							630.1	-30.6	No
8	km	Yr	m	Ht	km*Yr	km*m	km*Ht	Yr*m								623.2	-37.5	Yes

Number of Variables	X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11	X12	X13	X14	X15	AIC	Delta AIC	Select
8	km	Yr	m	Ht	km*Yr	km*m	km*Ht	m*Ht								625.7	-35.0	No
8	km	Yr	m	Ht	km*Yr	km*m	Yr*m	m*Ht								641.4	-19.3	No
8	km	Yr	m	Ht	km*Yr	km*Ht	Yr*m	m*Ht								623.0	-37.7	No
8	km	Yr	m	Ht	km*m	km*Ht	Yr*m	m*Ht								623.8	-36.9	No
7	km	Yr	m	Ht	km*Yr	km*m	km*Ht									620.4	-40.3	No
7	km	Yr	m	Ht	km*Yr	km*m	Yr*m									636.5	-24.2	No
7	km	Yr	m	Ht	km*Yr	km*Ht	Yr*m									617.3	-43.4	Yes
7	km	Yr	m	Ht	km*m	km*Ht	Yr*m									618.2	-42.5	No
6	km	Yr	m	Ht	km*Yr	km*Ht										614.6	-46.1	No
6	km	Yr	m	Ht	km*Yr	Yr*m										629.5	-31.2	No
6	km	Yr	m	Ht	km*Ht	Yr*m										612.0	-48.7	Yes
5	km	Yr	m	Ht	km*Ht											609.9	-50.8	Yes
5	km	Yr	m	Ht	Yr*m											621.8	-38.9	No
4	km	Yr	m	Ht												619.7	-41.0	No
4	km	Yr	Ht	km*Ht												605.2	-55.5	Yes
4	km	m	Ht	km*Ht												618.7	-42.0	No
3	km	Ht	km*Ht													614.0	-46.7	No
3	km	Yr	Ht													614.9	-45.8	No

APPENDIX D: AICC VALUES FOR ALL POSSIBLE MODELS WITH ONE AND TWO VARIABLES FOR THE NUMBER OF SHEEPSHEAD FORAGING INCIDENTS (NUMBER M^{-2} H^{-1})

APPENDIX D: Number of variables in the model, AICc, and Delta AICc for all possible models with one and two variables for the number of Sheepshead foraging incidents (number m^{-2} h^{-1}). X1 and X2 denote the variable(s). Delta AICc is the AICc for the model in each row minus the AICc of the final model (smallest AICc). Models are sorted in order of ascending AICc. DNC denotes that the model did not converge.

X1	X2	Number of Variables	AICc	Delta AICc (Row - Smallest)
DO	Time to Slack Tide	2	103.86	0.00
Stone Crabs	Algae	2	106.17	2.31
Barnacles	Algae	2	106.31	2.45
Algae	Depth	2	106.34	2.48
Algae	Bryozoa	2	107.61	3.75
Algae	DO	2	107.61	3.75
Sheepshead	Algae	2	108.19	4.33
Sheepshead	Hypoxia	2	108.24	4.38
Algae	Salinity	2	108.32	4.46
Barnacles	DO	2	108.39	4.53
Algae	Hypoxia	2	109.64	5.78
Algae	Location	2	109.93	6.07
Sheepshead	Bryozoa	2	109.97	6.11
Barnacles	Salinity	2	110.35	6.49
Algae	Temperature	2	110.69	6.83
Barnacles	Bryozoa	2	111.10	7.24
DO	Location	2	111.12	7.26
Stone Crabs	Time to Slack Tide	2	111.2	7.34
Barnacles	Depth	2	111.23	7.37
Algae	Time to Slack Tide	2	111.27	7.41
Barnacles	Hypoxia	2	111.38	7.52
Time to Dark	Algae	2	111.84	7.98
Barnacles	Location	2	111.91	8.05
Bryozoa	DO	2	112.02	8.16
DO	Depth	2	112.02	8.16
Sheepshead	DO	2	112.03	8.17
Sheepshead	Salinity	2	112.03	8.17

X1	X2	Number of Variables	AICc	Delta AICc (Row - Smallest)
DO	Hypoxia	2	112.11	8.25
Sheepshead	Barnacles	2	112.14	8.28
Stone Crabs	Salinity	2	112.27	8.41
Stone Crabs	Time to Dark	2	112.33	8.47
Barnacles	Temperature	2	112.37	8.51
Bryozoa	Depth	2	112.46	8.60
Hypoxia	Location	2	112.52	8.66
Sheepshead	Depth	2	112.71	8.85
Bryozoa	Location	2	113.12	9.26
Salinity	Temperature	2	113.13	9.27
Sheepshead	Temperature	2	113.24	9.38
Sheepshead	Location	2	113.25	9.39
Bryozoa	Hypoxia	2	113.30	9.44
Hypoxia	Depth	2	113.30	9.44
Stone Crabs	Sheepshead	2	113.59	9.73
Barnacles	Time to Slack Tide	2	113.63	9.77
Depth	Location	2	113.63	9.77
Bryozoa	Salinity	2	113.66	9.80
Temperature	Depth	2	113.66	9.80
Salinity	Depth	2	113.73	9.87
DO	Salinity	2	113.78	9.92
DO	Temperature	2	113.78	9.92
Time to Dark	Barnacles	2	113.79	9.93
Hypoxia	Time to Slack Tide	2	113.86	10.00
Bryozoa	Time to Slack Tide	2	113.92	10.06
Salinity	Location	2	114.05	10.19
Algae		1	114.09	10.23
Bryozoa	Temperature	2	114.27	10.41
Salinity	Hypoxia	2	114.37	10.51
Time to Dark	DO	2	114.42	10.56
Temperature	Hypoxia	2	114.97	11.11
Depth	Time to Slack Tide	2	114.97	11.11
Time to Dark	Bryozoa	2	115.37	11.51
Time to Dark	Depth	2	115.40	11.54
Temperature	Location	2	115.41	11.55
Time to Slack Tide	Location	2	115.45	11.59
Sheepshead	Time to Slack Tide	2	115.48	11.62

X1	X2	Number of Variables	AICc	Delta AICc (Row - Smallest)
Salinity	Time to Slack Tide	2	115.48	11.62
Temperature	Time to Slack Tide	2	115.64	11.78
Time to Dark	Sheepshead	2	115.95	12.09
Time to Dark	Hypoxia	2	115.96	12.10
Barnacles		1	116.02	12.16
Time to Dark	Salinity	2	116.06	12.20
Time to Dark	Location	2	116.48	12.62
DO		1	116.94	13.08
Algae	Time	2	117.06	13.20
Time to Dark	Temperature	2	117.16	13.30
Depth		1	117.62	13.76
Bryozoa		1	117.72	13.86
Time to Dark	Time to Slack Tide	2	117.92	14.06
Sheepshead		1	117.98	14.12
Hypoxia		1	118.47	14.61
Salinity		1	118.59	14.73
Location		1	118.91	15.05
Temperature	Time	2	119.38	15.52
Temperature		1	119.52	15.66
Barnacles	Time	2	119.53	15.67
DO	Time	2	119.98	16.12
Time to Slack Tide		1	120.17	16.31
Time to Dark		1	120.62	16.76
Sheepshead	Time	2	121.03	17.17
Bryozoa	Time	2	121.09	17.23
Time	Depth	2	121.28	17.42
Hypoxia	Time	2	121.38	17.52
Time	Location	2	122.02	18.16
Salinity	Time	2	123.14	19.28
Time	Time to Slack Tide	2	123.81	19.95
Time to Dark	Time	2	123.82	19.96
Time		1	126.09	22.23
Stone Crabs		1	DNC	
Stone Crabs	Barnacles	2	DNC	
Stone Crabs	Bryozoa	2	DNC	
Stone Crabs	DO	2	DNC	
Stone Crabs	Temperature	2	DNC	

X1	X2	Number of Variables	AICc	Delta AICc (Row - Smallest)
Stone Crabs	Hypoxia	2	DNC	
Stone Crabs	Time	2	DNC	
Stone Crabs	Depth	2	DNC	
Stone Crabs	Location	2	DNC	

APPENDIX E: AICC VALUES FOR ALL POSSIBLE MODELS WITH ONE AND TWO VARIABLES FOR THE TIME SHEEPSHEAD SPENT FORAGING (TIME M^{-2} H^{-1})

APPENDIX E: Number of variables in the model, AICc, and Delta AICc for all possible models with one and two variables for the time Sheepshead spent foraging (time m^{-2} h^{-1}). X1 and X2 denote the variable(s). Delta AICc is the AICc for the model in each row minus the AICc of the final model (smallest AICc). Models are sorted in order of ascending AICc. DNC denotes that the model did not converge.

X1	X2	Number of Variables	AICc	Delta AICc (Row - Smallest)
DO	Time to Slack Tide	2	186.11	0.00
Stone Crabs	Barnacles	2	188.48	2.37
Stone Crabs	Algae	2	189.11	3.00
Barnacles	Algae	2	190.45	4.34
Algae	Depth	2	190.64	4.53
Algae	Bryozoa	2	191.39	5.28
Algae	Salinity	2	192.15	6.04
Barnacles	Salinity	2	192.19	6.08
Stone Crabs	DO	2	192.65	6.54
Stone Crabs	Location	2	192.97	6.86
Stone Crabs	Salinity	2	193.02	6.91
Stone Crabs	Time to Slack Tide	2	193.14	7.03
Algae	DO	2	193.14	7.03
Stone Crabs	Depth	2	193.25	7.14
Stone Crabs	Bryozoa	2	193.43	7.32
Stone Crabs	Hypoxia	2	193.78	7.67
Sheepshead	Algae	2	193.99	7.88
Sheepshead	Bryozoa	2	194.30	8.19
Algae	Hypoxia	2	194.40	8.29
Algae	Location	2	194.45	8.34
Stone Crabs	Temperature	2	194.56	8.45
Barnacles	DO	2	194.60	8.49
Stone Crabs	Sheepshead	2	194.72	8.61
Stone Crabs	Time to Dark	2	195.21	9.10
Algae	Temperature	2	195.27	9.16
Algae	Time to Slack Tide	2	195.27	9.16
Salinity	Time to Slack Tide	2	195.35	9.24
Barnacles	Bryozoa	2	195.62	9.51

X1	X2	Number of Variables	AICc	Delta AICc (Row - Smallest)
DO	Salinity	2	195.88	9.77
Time to Dark	Salinity	2	196.00	9.89
Barnacles	Depth	2	196.01	9.90
Salinity	Hypoxia	2	196.01	9.90
Time to Dark	Algae	2	196.02	9.91
Bryozoa	Salinity	2	196.04	9.93
Salinity	Depth	2	196.08	9.97
Sheepshead	Salinity	2	196.11	10.00
Salinity	Location	2	196.38	10.27
Sheepshead	Temperature	2	196.45	10.34
Barnacles	Hypoxia	2	196.47	10.36
Barnacles	Location	2	196.56	10.45
Sheepshead	Hypoxia	2	196.59	10.48
Sheepshead	Barnacles	2	196.72	10.61
Barnacles	Temperature	2	196.98	10.87
DO	Location	2	197.10	10.99
Sheepshead	Depth	2	197.20	11.09
Bryozoa	DO	2	197.29	11.18
Bryozoa	Time to Slack Tide	2	197.39	11.28
Bryozoa	Depth	2	197.43	11.32
DO	Hypoxia	2	197.50	11.39
Bryozoa	Location	2	197.56	11.45
Salinity	Temperature	2	197.58	11.47
Sheepshead	DO	2	197.68	11.57
Bryozoa	Hypoxia	2	197.76	11.65
DO	Depth	2	197.83	11.72
Barnacles	Time to Slack Tide	2	197.91	11.80
Sheepshead	Location	2	198.06	11.95
Time to Dark	Barnacles	2	198.41	12.30
Hypoxia	Depth	2	198.55	12.44
Hypoxia	Location	2	198.58	12.47
Temperature	Depth	2	198.64	12.53
Depth	Location	2	198.65	12.54
Bryozoa	Temperature	2	198.90	12.79
Time to Slack Tide	Location	2	198.99	12.88
Hypoxia	Time to Slack Tide	2	199.18	13.07

X1	X2	Number of Variables	AICc	Delta AICc (Row - Smallest)
Depth	Time to Slack Tide	2	199.20	13.09
DO	Temperature	2	199.30	13.19
Sheepshead	Time to Slack Tide	2	199.41	13.30
Time to Dark	DO	2	199.62	13.51
Stone Crabs	Time	2	199.65	13.54
Time to Dark	Bryozoa	2	199.65	13.54
Temperature	Hypoxia	2	200.10	13.99
Temperature	Time to Slack Tide	2	200.16	14.05
Time to Dark	Depth	2	200.18	14.07
Temperature	Location	2	200.19	14.08
Time to Dark	Sheepshead	2	200.60	14.49
Time to Dark	Hypoxia	2	200.81	14.70
Time to Dark	Location	2	200.93	14.82
Time to Dark	Temperature	2	201.37	15.26
Algae	Time	2	201.66	15.55
Time to Dark	Time to Slack Tide	2	202.15	16.04
Stone Crabs		1	203.19	17.08
Algae		1	204.26	18.15
Barnacles	Time	2	204.30	18.19
Temperature	Time	2	204.81	18.70
Bryozoa	Time	2	205.94	19.83
DO	Time	2	205.96	19.85
Sheepshead	Time	2	206.03	19.92
Salinity	Time	2	206.25	20.14
Barnacles		1	206.32	20.21
Time	Depth	2	206.38	20.27
Salinity		1	206.82	20.71
Hypoxia	Time	2	206.88	20.77
Time	Location	2	207.01	20.90
Bryozoa		1	208.09	21.98
DO		1	208.35	22.24
Time	Time to Slack Tide	2	208.37	22.26
Depth		1	208.38	22.27
Sheepshead		1	208.44	22.33
Time to Dark	Time	2	208.55	22.44
Hypoxia		1	209.28	23.17

X1	X2	Number of Variables	AICc	Delta AICc (Row - Smallest)
Location		1	209.36	23.25
Temperature		1	209.93	23.82
Time to Slack Tide		1	210.08	23.97
Time to Dark		1	210.48	24.37
Time		1	216.71	30.60

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VITA

David Reeves was born in Homewood, Alabama to Glenn and Claire Reeves. His family moved to Fairhope, Alabama when David was a child and he immediately became infatuated with the critters living in the Gulf of Mexico. David graduated from Bayside Academy in 2008 and enrolled at Loyola University New Orleans. While at Loyola, he was mentored by Frank Jordan and completed an undergraduate thesis about Okaloosa Darter utilization of stream restorations. David graduated from Loyola with a Bachelor of Science in biological sciences in 2012. In 2012, he began working on a Master of Science in oceanography and coastal sciences at Louisiana State University under the direction of Ed Chesney and Don Baltz. He defended his thesis comparing reef-associated organisms at platforms on and around Ship Shoal in March of 2015 and graduated in the subsequent May. Sometime after David received his Master's in 2015, Ed Chesney began to fear that David would pursue a Ph.D. at Ohio State University. Ed, being a loyal Wolverine, could not tolerate that and convinced David to stay at LSU to pursue a Ph.D. David is expecting to graduate from LSU in May of 2018.